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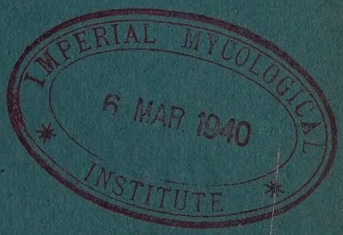

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MATHÉMATIQUES

SUR UNE CLASSE DE POINTS SINGULIERS ESSENTIELS

Par N. LAMBIN

(Présenté par A. N. Kolmogoroff, de l'Académie, le 16. VIII. 1939)

Soit $f(z)$ une fonction holomorphe sur un ensemble connexe L du plan ou de la surface de Riemann, $f(z) \neq 0$, $f'(z) \neq 0$, $\arg f(z) = \text{const}$; on suppose que l'ensemble L n'est pas une partie d'un ensemble L_1 jouissant des mêmes propriétés; dans ce cas nous dirons que l'ensemble L est une ligne de gradient de la fonction $f(z)$.

Ainsi une ligne de gradient de $f(z)$ est, en général, une partie d'une ligne d'argument constant de $f(z)$ [1]. Il est évident qu'une ligne de gradient n'a pas de points multiples et que deux lignes de gradient ne se coupent pas. Nous prendrons pour direction sur la ligne de gradient celle pour laquelle $|f(z)|$ croît.

On nomme extrémité (origine) de la ligne de gradient L un point z_0 du plan z tel que chaque voisinage de ce point contient tous les points de la ligne de gradient L, pour lesquels les valeurs de $|f(z)|$ sont suffisamment grandes (petites) ou bien les valeurs de $|f(z)|$ sont assez proches de la borne exacte supérieure (inférieure) de $|f(z)|$ sur L.

On peut démontrer que chaque ligne de gradient d'une fonction univalente, ayant au plus une infinité dénombrable de points singuliers essentiels, a une extrémité et une origine. Par une fonction qui n'est pas univalente ce théorème n'est pas vrai, parce que la surface riemannienne dans ce cas n'est pas compacte.

Etudions un point singulier essentiel z_0 d'une fonction analytique $f(z)$ tel qu'au voisinage de ce point $f(z)$ est univalente, ne s'annulle pas et possède une dérivée qui n'est pas nulle. L'étude d'un point singulier essentiel isolé dans le cas général peut être réduite à ce cas par la substitution

$$f(z) = e^{A\int_a^z e^{\Phi(t)}dt}$$

A étant choisi de telle manière que le résidu de la fonction $Ae^{\Phi(z)}$ au point z_0 soit un nombre entier.

Chaque ligne de gradient ayant des points communs avec un voisinage D d'un point singulier essentiel de la nature considérée joint ou bien deux points du contour Γ de ce voisinage, ou bien un point de la courbe Γ et le point z_0, ou bien commence et finit au point z_0. On suppose ici que le voisinage du point z_0 est un domaine arbitraire simplement connexe contenant le point z_0 et borné par une courbe fermée rectifiable de Jordan. En classifiant les

points du domaine D suivant le critère qui vient d'être indiqué, on peut constater que si Γ est convenablement choisi, le domaine D peut être divisé par un nombre fini ou une infinité dénombrable de lignes de gradient en domaines de la forme suivante:

1. Domaine borné par des lignes de gradient ayant leur origine et leur extrémité au point z_0, représenté par la fonction $\ln f(z)$ sur un demi-plan borné par une droite parallèle à l'axe réel (domaine du type d'un demi-plan).

2. Domaine borné par des lignes de gradient qui ont leur origine et leur extrémité au point z_0, représenté par la fonction $\ln f(z)$ sur une bande bornée par deux droites parallèles à l'axe réel (domaine du type d'une bande).

3. Domaine borné par deux segments de lignes de gradient joignant z_0 à la ligne Γ, par un segment de la ligne Γ qui est en même temps un segment d'une ligne isomodulaire de $f(z)$ [d'une ligne $|f(z)|=C$] et, peut-être, par des lignes de gradient qui ont leur origine et leur extrémité au point z_0; un tel domaine est représenté par la fonction $\ln f(z)$ sur une partie de la bande précédemment indiquée, partie située à droite ou à gauche d'une certaine droite parallèle à l'axe imaginaire (domaine du type d'une demi-bande).

4. Domaine borné par deux segments de lignes de gradient joignant z_0 à la ligne Γ, par un segment de la ligne Γ, formé de deux segments de lignes isomodulaires et par un segment d'une ligne de gradient et, peut-être, de lignes de gradient qui ont leur origine et leur extrémité au point z_0; un tel domaine est représenté par la fonction $\ln f(z)$ sur un rectangle (domaine du type d'un rectangle).

Le procédé même de division peut être choisi de telle manière qu'aucun de ces domaines ne soit une partie d'un autre domaine de l'un quelconque des types considérés, même s'il est obtenu par un autre mode de division du domaine D.

Les domaines que l'on obtient de cette manière seront nommés caractéristiques.

On peut démontrer, que le voisinage D étant donné, la division en domaines caractéristiques est unique, et que les valeurs asymptotiques de $f(z)$ peuvent être obtenues, quand on s'approche de z_0 en suivant les contours des domaines caractéristiques.

Théorème I. *Si les fonctions $F(z)$ et $f(z)$ ont au point z_0 un point singulier essentiel du type étudié, et si pour un choix convenable des voisinages correspondants les ensembles des contours des domaines caractéristiques de $F(z)$ et de $f(z)$ sont topologiquement égaux, si les valeurs asymptotiques atteintes sur les parties correspondantes de ces contours sont égales, et les modules de ces valeurs asymptotiques sont atteints de la même manière, c'est-à-dire tous les deux d'en-haut ou tous les deux d'en-bas, si enfin les domaines correspondants du type d'une bande ou du type d'une demi-bande sont représentés sur des bandes ou des demi-bandes de largeur égale, on a l'identité*

$$F(z)=f[\varphi(z)] \tag{1}$$

où $\varphi(z)$ est une fonction analytique au point z_0

$$\varphi(z_0)=z_0 \quad et \quad \varphi'(z_0)\neq 0.$$

L'application de ce théorème à des classes plus restreintes de fonctions donne

Théorème II. *Si $f(z)$ possède en z_0 un point singulier essentiel du type étudié et n'a pour valeurs asymptotiques que 0 et ∞, on a*

$$f(z)=(z-z_0)^k e^{p(z)} \tag{2}$$

où $p(z)$ a un pôle au point z_0 et k est un entier positif.

Théorème III. *Supposons que $f(z)$ a en $z_0=\infty$ un point singulier essentiel du type étudié et n'a pour valeurs asymptotiques que $0, \infty$ et 1. Supposons d'ailleurs qu'il n'existe pas deux chemins topologiquement différents, suivant lesquels on atteint la valeur asymptotique 1, c'est-à-dire que chaque courbe, suivant laquelle on atteint la valeur asymptotique 1, peut être transformée en chaque autre courbe de cette sorte par une déformation continue, et d'ailleurs que pendant toute la déformation la courbe conserve cette propriété que la valeur 1 est asymptotiquement atteinte suivant cette courbe. On a alors l'identité*

$$f(z)=Me^{N\int_p^{\varphi(z)}\frac{(t-a)^m}{(t-b)^n}e^t dt} \tag{3}$$

où $\varphi(z)$ possède au point $z_0=\infty$ un pôle du premier ordre, et M, N, a, b, m et n sont des constantes convenablement choisies et qui dépendent de la forme de $f(z)$. Les nombres m et n sont entiers, $m \geqslant 0$, $n \geqslant 0$.

Manuscrit reçu
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[1] Lucien Hilbert, C. R., **205**, 1121 (1937), **207**, 962 (1938); Georges Valiron, C. R., **208**, 711.

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MATHÉMATIQUES

LA MÉTHODE DE M. PERRON POUR L'INTÉGRALE DE M. DENJOY

Par G. TOLSTOFF

(Présenté par A. N. Kolmogoroff, de l'Académie, le 15. IX. 1939)

P. S. Alexandroff a démontré que l'intégration au sens de Perron est équivalente à celle que l'on nomme intégration restreinte au sens de Denjoy (1). Il est naturel de poser la question: est-il possible de donner une définition de l'intégrale qui «contienne» celle de l'intégrale générale de Denjoy (2)?

I. Ridder a proposé plusieurs définitions de cette nature (3,4,5). Cependant le problème posé ne peut pas être considéré comme complètement résolu: les majorantes et minorantes qui figurent dans la définition de Perron sont liées à la fonction que l'on intègre au moyen de l'opération de dérivation, tandis que les majorantes et minorantes dans les définitions de Ridder sont liées à la fonction que l'on intègre au moyen d'autres opérations qui ressemblent en quelque sorte à la dérivation. Il y a des raisons à considérer cette ressemblance comme assez éloignée.

En effet, considérons l'une des définitions de majorantes de Ridder, celle qui, à mon avis, ressemble plus que les autres à la définition de Perron.

Une fonction $\varphi(x)$ est nommée majorante pour une fonction $f(x)$ définie sur $[a, b]$, si elle jouit des propriétés suivantes:

a) $\varphi(a)=0$; b) $\varphi(x)$ est continue sur $[a, b]$; c) tout le segment $[a, b]$, sauf peut-être une infinité dénombrable de ses points, peut être couvert par une infinité dénombrable d'ensembles parfaits E_i $(i=1, 2, 3, \ldots)$ tels que sur chacun de ces E_i la dérivée inférieure de $\varphi(x)$, prise par rapport à cet ensemble, est supérieure ou égale à $f(x)$ et diffère de $-\infty$.

Désignons par $D_{E_i}\varphi(x)$ la dérivée inférieure de $\varphi(x)$ prise par rapport à l'ensemble E_i. Un point x de $[a, b]$ appartient, en général, à plusieurs ensembles E_i recouvrant $[a, b]$. Soient $E_{n_1}(x), E_{n_2}(x), \ldots, E_{n_k}(x), \ldots$ ces ensembles. Il correspond ainsi au point x les nombres

$$\underline{D}_{E_{n_1(x)}}\varphi(x), \underline{D}_{E_{n_2(x)}}\varphi(x), \ldots, \underline{D}_{E_{n_k(x)}}\varphi(x), \ldots$$

On construit facilement des exemples de fonctions et de recouvrements du segment $[a, b]$ tels qu'il existe une infinité non-dénombrable de valeurs de x, pour chacune desquelles au moins deux des nombres de la suite considérée sont différents (cependant, on peut démontrer que presque pour toutes les valeurs de x tous les nombres de cette suite coïncident).

Ainsi dans cette définition de Ridder il n'est pas très commode de donner à $\underline{D}_{E_i}\varphi(x)$ le nom de dérivée inférieure généralisée de $\varphi(x)$, puisque aux points, où elle est définie, ces valeurs définissent non seulement $\varphi(x)$, mais toute une famille de fonctions.

Dans la présente Note je vais indiquer une dérivation généralisée qui diffère peu de la dérivation de Ridder que nous venons de considérer, mais qui conduit à une dérivée déterminée d'une manière unique partout sur $[a, b]$, sauf peut être en un ensemble dénombrable de points.

Cette dérivation permet de résoudre au sens positif le problème précédemment posé.

Définition 1. Une fonction $\Phi(x)$ est appelée (D)-dérivable sur un segment $[a, b]$, si elle est continue sur $[a, b]$ et s'il est possible de couvrir $[a, b]$ par une infinité dénombrable d'ensembles parfaits, tel que sur chacun d'eux $\Phi(x)$ est dérivable par rapport à cet ensemble *. On peut démontrer la proposition suivante:

Lemme 1. Si $\Phi(x)$ est (D)-dérivable sur $[a, b]$ et si

$$[a, b] = \sum_{n=1}^{\infty} P_n$$

où P_n sont les ensembles parfaits qui figurent dans la définition 1, l'ensemble des points x pour lesquels

$$\Phi'_{P_i}(x) \neq \Phi'_{P_j}(x)$$

au moins pour un couple d'indices (i, j) est au plus dénombrable. [On désigne ici par $\Phi'_{P_n}(x)$ la dérivée ordinaire au point x prise par rapport à l'ensemble P_n, et l'on suppose d'ailleurs que $x \subset P_n$].

Définition 2. On appelle dérivée d'une fonction $\Phi(x)$ D-dérivable sur $[a, b]$ la fonction $(D)\Phi(x)$ définie d'une manière unique partout sur $[a, b]$, sauf au plus pour un ensemble dénombrable E (voir le lemme 1), par l'égalité

$$(D)\Phi(x) = \Phi'_{P_n}(x),$$

où P_n est l'un quelconque des ensembles parfaits figurant dans la définition 1.

Il est facile à déduire de ces définitions les propriétés essentielles de la dérivation (D) et de la (D)-dérivée, propriétés qui ressemblent à celles de la dérivation ordinaire.

Définition 3. Une fonction $\varphi(x)$ est appelée majorante par une fonction $f(x)$ définie sur $[a, b]$, si $\varphi(x)$ est continue et (D)-dérivable sur $[a, b]$, $\varphi(a) = 0$ et $(D)\varphi(x) \geqslant f(x)$, $(D)\varphi(x) > -\infty$ en tous les points $x \subset [a, b]$, sauf au plus en un ensemble dénombrable.

Définition 4. Une fonction $\psi(x)$ est appelée minorante pour $f(x)$, si $\psi(a) = 0$, $\psi(x)$ est continue et (D)-dérivable sur $[a, b]$, et si $(D)\psi(x) \leqslant f(x)$, $(D)\psi(x) < +\infty$ en tous les points, sauf au plus en un ensemble dénombrable.

On démontre aisément le lemme suivant:

Lemme 2. Si $\varphi(x)$ est une majorante pour $f(x)$ et $\psi(x)$ est une minorante, $\varphi(x) - \psi(x)$ est non-décroissante sur $[a, b]$. Il en résulte que

$$\sup \psi(x) \leqslant \inf \varphi(x)$$

---

* La valeur de la dérivée peut être finie ou infinie.

pour chaque x appartenant au segment $[a, b]$, où l'on désigne par $\sup \psi(x)$ la borne supérieure des valeurs de toutes les minorantes au point x, et $\inf \varphi(x)$ désigne la borne inférieure des valeurs de toutes les majorantes au point x. Il est évident que la différence $\inf \varphi(x) - \sup \psi(x)$ est non-décroissante.

Donc, si l'on a

$$\inf \varphi(b) = \sup \psi(b) \tag{1}$$

il en résulte

$$\inf \varphi(x) = \sup \psi(x) \tag{2}$$

quel que soit x sur $[a, b]$.

Définition 5. Une fonction $f(x)$ définie sur $[a, b]$ est nommée intégrable sur ce segment, si pour ses majorantes et minorantes on a la relation (1). On prend pour valeur numérique de l'intégrale la valeur commune des quantités qui figurent dans l'égalité (1).

La relation (2) prouve que l'intégrabilité sur $[a, b]$ entraîne l'intégrabilité sur $[a, x]$ pour $a \leqslant x \leqslant b$.

En tenant compte de la définition 5, on peut énoncer la proposition fondamentale suivante:

Pour qu'une fonction $f(x)$ définie sur $[a, b]$ soit intégrable au sens de l'intégrale générale de Denjoy, il faut et il suffit qu'elle soit intégrable au sens de la définition 5.

La démonstration de cette proposition est assez longue, c'est pourquoi elle paraîtra ailleurs.

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PHYSICS

A NEW METHOD OF MICROSCOPY IN ULTRA-VIOLET RAYS

By E. M. BRUMBERG

(Communicated by S. I. Wawilow, Member of the Academy, 26.V.1939)

When the microscopic slide possesses natural coloration, one usually can judge of the nature of its coloured parts directly by their appearance. Thus, for example, using sufficient magnification green chlorophyll plastids can be identified on a section of a leaf, or white and red corpuscles of the blood can be distinguished from each other. However, the strong selective absorption in the visual region of the spectrum, which is necessary to obtain clearly visible coloration in thin layers, is relatively rare both in living and non-living kingdoms. Biologists have, therefore, to stain their slides with special stains which are subject to selective absorption by different tissues of a section. Such staining necessitates the introduction into the material of foreign substances which are liable to alter the natural conditions which previously existed there; it requires, moreover, much time and skill while good results are far from being always obtained.

Certain additional possibilities are offered by luminescence microscopy which makes it possible to draw certain conclusions on the chemistry of the details of a slide from their own luminescence produced by ultra-violet rays, however, this method is not universal either, since only a few substances possess the property of luminescence.

To differentiate microscopic objects photography in ultra-violet rays was recently applied in addition to the previously known methods of microscopy. The first microscope with optical equipment made of quartz and destined for microphotography in ultra-violet was designed by A. Köhler in 1904 (1). The original aim of the design of this instrument was to raise the resolving power of the microscope; following the well known Abbé's formula, this may be attained by reducing the wave length of the light which serves to illuminate the material under observation. It appeared later on that microphotographs made in ultra-violet rays were distinguished by possessing more contrasts owing to strong absorption of the short-wave radiation; this method became, therefore, interesting by itself for discriminating finer details of the preparations. This latter is at present the principal aim of the ultra-violet microscopy.

The first object lenses of Zeiss were quartz monochromates intended for the wave length of the bright line of the spark spectrum of magnesium 280 mμ, or of the cadmium lines 275 and 214 mμ. Quite recently the same makers have computed and constructed a quartz fluorite achromate with the aid of which one can comfortably and accurately focuse the preparation

in the visible light, to pass next to the photography using the desired region of the spectrum, by merely changing the length of the wave of the light which serves to illuminate the preparation.

The possibility of a much greater differentiation of the elements of the object by applying photography in ultra-violet rays depends on the fact that in the majority of substances the main intense absorption lines are located in this very region of the spectrum; the regions of continuous absorption sharply delimited from those with greater wave length, begin here, too. Thus, if the eye was able to see ultra-violet radiation and experience colour-sensation in this region, under a microscope equipped with quartz lenses one would see slides in colours.

The method advanced by us is a combination of microphotography in ultra-violet rays with examination of photographs in colours. It consists in the following.

Three photographs are made in a sequence with the aid of a microscope equipped with quartz lenses and a quartz monochromator which allows changing the wave length of the light applied for illumination of the slide. The photographs obtained (negative or positive copies) are projected at the one and the same place of the screen with the aid of three projecting devices; each of them is supplied with a colour screen which lets pass one of the three basic colours: red, green or blue.

When the image accurately coincide, a colour picture arises on the screen: the colours of its elements depend on the difference in the density of the corresponding places of the photographs and, consequently, *ceteris paribus*, on the character of absorption in the preparation. This scheme of production of colour photographs is similar to that of the three-colour additive method of colour photography (now obsolete). It differs from it only in that no reproduction of natural coloration is aimed at in this case; the colours of the picture are conventional and arbitrary ones, depending on the choice of colour screens used for examination*. For practical purposes it is more convenient, instead of projecting three negatives onto a screen, to use one of the known types of chromoscopes formerly applied for a similar purpose in colour photography.

The choice of wave length depends upon the character of absorption of the objects to be examined. Sometimes it is advisable to make one of the photographs in visible light or in infra-red; in other cases two photographs may be selected arbitrarily, but in order to attain reproducible results their choice must be decided upon in advance.

The character of absorption in individual elements of the preparation photographed in the light of different wave length can be determined by a simple comparison of the black-and-white pictures or, with more precision, by means of measurement of the density of the corresponding places on the negatives with the aid of a microphotometer; the latter method is actually used in some cases. The use of the microphotometer gives sometimes a sensitivity which exceeds that attained by the above method of colour perception when slight differences are determined. The colour method has, however, a number of advantages over the «black-white» one in other respects, too. Its principal merit consists in the fact that it makes unnecessary a very laborious comparison of the photographs spot by spot and makes it possible to see at once on a single image the distribution of different materials or to count

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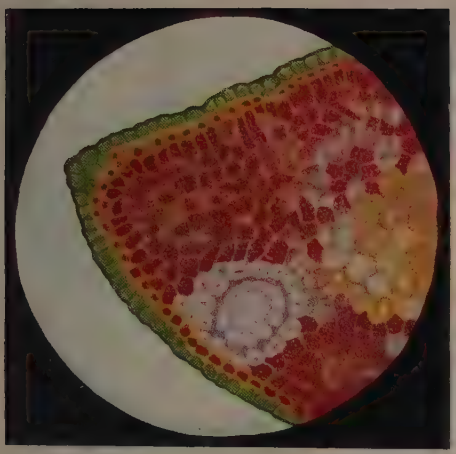
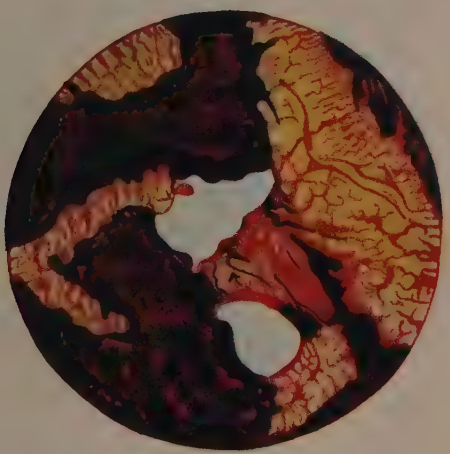
* This method makes it also possible to obtain colour photographs with the aid of the electron microscope by taking subsequent photographs at different electron velocities. In this case we shall similarly obtain a conventional colour characteristic of the object for the cathode rays.



Фиг. 1. Поперечный срез иглы хвои сосны. Длина волн при съемке: 400 mμ, 300 mμ, 250 mμ. Фильтры при наблюдении: зеленый, красный, синий.

Fig. 1. Cross-section of a pine needle. Photographed at a wave length of 400 mμ, 300 mμ, 250 mμ. Green, red and blue filters.



Фиг. 2. Шлиф метаморфически измененного гранита. Съемка: 400 mμ, 300 mμ, 250 mμ. Фильтры при наблюдении: зеленый, красный, синий.

Fig. 2. Slice of a metamorphously altered granite. Photographed at 400 mμ, 300 mμ, 250 mμ. Green, red, blue filters.

Фиг. 3. Мономинеральный шлиф циркона. Съемка: 350 mμ, 300 mμ. Фильтры при наблюдении: зеленый, красный.

Fig. 3. Monomineral slice of zircon. Photographed at a wave length of 350 mμ and 300 mμ. Green and red filters.

the number of identical elements (analysis of the composition of powdered materials). The colour method reveals also slight local changes in the density, which otherwise could be made only by means of exact photometry. Lastly the colour method is less sensitive to changes in exposure and to the regime of development, and, therefore, requires a less strict standartization of the conditions of photographing. Slight underexposures or overexposures, overdeveloping or underdeveloping, may, indeed, be in this case easily compensated for by a corresponding change in the brightness of light source used for the illumination of the deficient negative. The necessary relation of brightness of illumination of individual photographs is checked by inspecting empty areas of the slide or holes in the section of the object; in case of correct illumination these should be colourless.

Naturally, such a compensation is possible only in case when the density of the photographs lies within the straight line part of the sensitometric characteristic of the photographic plate. Slight departures from the required relation between the illumination of the individual negatives introduce,

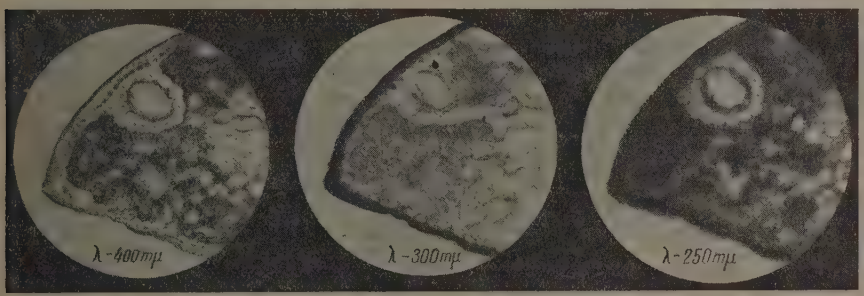


Fig. 4.

however, no material fault into the estimation of the colour shades, since the latter are merely compared with the surrounding objects. A slight surplus in brightness of the one of the three colour images corresponds approximately to the change in the spectral distribution of energy in the source of light when ordinary paper colour pictures are viewed, for example, to a change from daylight to the light of an electric lamp.

In Fig. 1, 2, 3 are presented samples of photographs obtained by the method described above. A high voltage spark between cadmium electrodes served as light source. The spectral regions in the ultra-violet part were isolated with the aid of a slitless quartz monochromator. As object lens was used Zeiss' quartz monochromat for $\lambda = 250$ mμ (6 mm; 0.35). The drawings for print were made by E. A. Derevizkaja in part from the screen, in part from observation through the chromoscope.

In Fig. 4 are given three copies from negatives, which were used to obtain the coloured copy (Fig. 1). They permit to judge of the severe changes of light absorption in the ultra-violet region with the change of its wave-length.

In concluding we would like to point out another interesting possibility of obtaining colour images in ultra-violet rays with the aid of fluorescence. A fluorescent screen should be inserted into the eyepiece, at the level of the image; the colour of fluorescence of this screen should be strictly connected with the wave length of the falling ultra-violet rays. Such a screen can be prepared by covering a transparent plate with a mixture of substances diffe-

ring both in colour of fluorescence and in the position of active bands of absorption. In accordance with the three-colour vision scheme one should take a mixture of three substances showing fluorescence of three basic colours. One may also use for this purpose three superimposed thin plates of fluorescent glass; they should be arranged in such a way that the plate turned toward the object lens of the microscope respond to the ultra-violet radiation of the shortest wave length and transmit that of the medium and long wave length; the next plate should react to the waves of medium length and transmit the long ones; finally, the last should absorb the ultra-violet radiation of the longest wave.

The application of three-colour fluorescent screens would considerably facilitate observations as it makes photographing unnecessary.

Screens prepared in the two ways described above show strong coloured shadows from transparent objects placed between them, and a high-voltage spark. It is possible, for instance, in this way to quickly determine, without using a spectrograph, by the colour of the shadows certain minerals, to distinguish different sorts of glass, etc.

The use of three-colour fluorescent screens in microscopy is possible only provided achromatic (still better apochromatic) objectives for the ultra-violet region of the spectrum are available. At the present at the State Optical Institute microscope achromates of different powers are being designed; their construction will enable us to study in detail the production of fluorescent screens for colour observations with the quartz microscope.

In the present work took part V. D. Mikhalevsky who has made some of the accompanying illustrations. The work is being done under the guidance of S. I. Wawilow, Member of the Academy, to whom my profound gratitude is due for the vivid interest in this topic and for his most valuable assistance in its development.

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BIOCHEMISTRY

ALTERATION IN THE ALKALOID COMPOSITION DUE TO THE INFLUENCE OF STOCK UPON SCION IN *NICOTIANA*

By A. SHMUCK, D. KOSTOFF and A. BOROZDINA

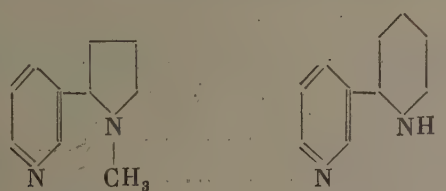
(Communicated by N. I. Vavilov, Member of the Academy, 3. X. 1939)

Studies on the effect of stock upon scion were up to the present time concerned with the morphological modification occurring in grafted plants. Considerably fewer are those investigations which demonstrate the regularities in alterations of the chemical composition of the stock and scion; in some instances there was established transfer of substances, for example of alkaloids ([1],[2]) or glucosides ([3]), in other it was not the case, for example the behaviour of inuline ([4]).

According to Krenke ([5]), formation of new characters in the scion may be the result of the influence of hidden properties of the scion itself which get under new developmental conditions a chance of a clear manifestation; they are not due to direct transmission from the stock.

It appeared of interest to study the modifications in the chemical properties of the alkaloids in grafted plants of *Nicotiana tabacum* and *Nicotiana glauca*.

N. tabacum is known to contain nicotine as the principal alkaloid which is usually accompanied with a small amount of accessory alkaloids, among which Ehrenstein ([6]) and others had identified anabasine. *Nicotiana glauca*, as first established by our studies, contains no nicotine but produces instead anabasine ([7],[8]).



nicotine anabasine

A. Shmuck and A. Borozdina have worked out a precise method which permits of a qualitative determination of the two alkaloids when they are present together. The method is based on the treatment of the mixture of the alkaloids (which are extracted from the plant with the aid of ether) with nitrous acid; nicotine remains intact after this treatment, whereas anabasine is transformed into nitroso-anabasine which loses its ability to react with picric acid, while nicotine reacts in the usual way and may be determined after Pfyl ([9]). The method is a very exact one; nevertheless, the results of the analyses were checked by means of another colorimetric reaction for anabasine and nicotine which was discovered by us.

If an aqueous solution of nicotine or anabasine is made to react with a solution of bromerhodan in the presence of aniline-water, both alkaloids produce a characteristic yellow coloration which sets in even when the concentrations of the alkaloids are extremely low. When coloured solutions are alkalinized with soda, the nicotine remains yellow, whereas the anabasine becomes vivid pink. This reaction makes it possible to distinguish qualitatively the alkaloids from each other and offers an expedient method of colorimetric quantitative determination of the two alkaloids.

Generative first generation hybrids between *N. glauca* and *N. tabacum*, as shown by our studies, contain no nicotine at all, but produce only anabasine. This law of inheritance of anabasine and nicotine was verified later in a number of studies ([10],[11]). We may consider as entirely proved that in plants of the first generation of a cross between plants bearing anabasine and nicotine only anabasine is present.

Experiments on grafting *N. tabacum* on *N. glauca* and vice versa were arranged by D. Kostoff with the aim to study transformations which take place in the alkaloid complex of the plants. Plants grafted on each other were grown for 50—60 days; then scion and stock were collected separeately and analyzed: leaves of various levels were analyzed, as well as the uppermost and the lowest portions of the stems of the stock and scion. In some of the experiments the leaves of the stock were removed immediately upon grafting in order to stop formation of alkaloids in the stock.

The control plants of *N. tabacum* and *N. glauca* which were grown under the same conditions as grafted ones, contained the following amount of alkaloids:

	Anabasine, %	Nicotine, %
N. tabacum:		
Stems	no	0.43
Leaves	no	0.74
N. glauca		
Stems	1.13	no
Leaves	0.79	no

The distribution of the alkaloids in plants grafted on each other was the following one:

		Anabasine	Nicotine
	I. *N. tabacum*, scion *N. glauca*, stock (without leaves)	% of the absolute dry weight	
Stock *N. glauca*	Stems (leaves of the stock removed) . .	0.07	traces
Scion *N. tabacum*	Stems, lower portion	0.19	no
	» upper »	0.12	»
	Leaves, lower	0.53	»
	» upper	0.23	»
	II. *N. tabacum*, scion *N. glauca*, stock (leaves of the stock left intact)		
Stock *N. glauca*	Lower part of the stem	0.22	traces
	Upper » » » »	0.17	»
	Upper leaves	2.27	0.02
	Lower »	2.11	0.07
Scion *N. tabacum*	Stems	0.58	no
	Leaves	0.86	»

The analyses clearly show that in the case when *N. tabacum* is grafted on *N. glauca* an extremely strong change in the alkaloid composition takes place. Scion of *N. tabacum* entirely loses its typical ability of accumulating nicotine and contains only anabasine, i. e. the alkaloid of its stock.

This result can by no means be attributed to the transference of anabasine from stock to scion, since the amount of anabasine in the scion *N. tabacum* was comparatively large and the leaves of tobacco contained more anabasine than the stem of tobacco, even in those cases when the leaves of the stock *N. glauca* were removed, and consequently the process of anabasine formation was supressed, as shown by the extremely low anabasine content in the stem of *N. glauca*. It follows that in the grafted tobacco leaves there occurs synthesis of anabasine instead of nicotine.

The same disturbance of the usual process of alkaloid production in tobacco and accumulation of anabasine instead of nicotine took place also when the stock *N. glauca* was left with its leaves and, consequently, when a normal synthesis of anabasine was going on in it. However, in this case formation of anabasine in the scion of tobacco became more intense and even exceeded that in the control tobacco plant grown under usual conditions.

All the above said testifies to a profound disturbance of the process of synthesis of the alkaloid in the grafted tobacco and to a strong effect of the stock upon the scion.

Curiously enough, nicotine was present in the system of the grafted plants in a quite negligible amount and could be detected only in the stock *N. glauca*, in which it could never be detected before when the species in question was growing under normal conditions. The distribution of nicotine in the stock (*N. glauca*) was a rather uniform one, both in stems and in leaves; this showed that nicotine was not synthesized in the stock, but has spread from the scion (*N. tabacum*).

In the grafted plants, both in stock and scion, anabasine most strongly dominates over nicotine, which reminds the first generation of generative hybrids between *N. tabacum* and *N. glauca* where anabasine also completely dominates over nicotine.

Somewhat different relations in the alkaloid content were observed when *N. tabacum* served as stock, and *N. glauca* as scion. When both stock and scion were left with their leaves, the presence of the two alkaloids was observed both in stock and scion.

III. *N. tabacum*, stock *N. glauca*, scion			Anabasine	Nicotine
			% of the absolute dry weight	
Stock	*N. tabacum*	Stems	1.29	0.87
		Leaves	0.66	1.89
Scion	*N. glauca*	Stems	1.86	0.11
		Leaves	3.24	0.01

Attention is attracted by a greater accumulation of anabasine in the leaves of *N. glauca* grafted on tobacco as compared with the control plant of *N. glauca*. The nicotine content in the grafted *N. glauca* was quite insignificant; it is very probable that it got into the scion by diffusion from the stock (*N. tabacum*), since the nicotine content in the leaves of *N. glauca* was ten times lower than that in the stem. Such a distribution of the alkaloids is quite unusual for a normally growing plant.

The stock (*N. tabacum*) contains both in stems and in leaves the two alkaloids, the anabasine prevailing in stems and the nicotine in leaves. This seems to point to that *N. tabacum* preserves its usual type of synthesis of nicotine and that anabasine is brought in only by diffusion from the scion; it is, therefore, considerably more abundant in the stem of tobacco than in the leaves.

When leaves were removed from the stock *N. tabacum*, the course of accumulation of alkaloids was a somewhat different one:

IV. *N. tabacum*, stock			Anabasine	Nicotine
			% of the absolute dry weight	
Stock	*N. tabacum*	Stems (leaves removed)	0.66	0.19
Scion	*N. glauca*	Stems	1.55	0.01
		Leaves	2.69	0.02

In the scion *N. glauca* there occurred normal formation of anabasine; the amount of the alkaloid formed was also higher than in the control plant and the influence of the stock was expressed only in the presence of a very insignificant amount of nicotine contained both in the stem of the stock (*N. tabacum*) and in the stems and leaves of *N. glauca*. The scion *N. glauca* in its turn effected the accumulation of a considerable amount of anabasine in the stem of the stock (*N. tabacum*).

The studies reported above quite definitely testify to an extremely strong influence of the grafted plants upon each other in respect to the process of accumulation of alkaloids. The following regularities in this phenomenon may be pointed out.

1. The grafted plants often accumulate considerably greater amounts of alkaloids than the control plants.

2. In the grafted *N. glauca* anabasine formation strongly prevails over nicotine formation: this recalls the dominance of anabasine in the first generation of generative hybrids.

3. A complete replacement of nicotine by anabasine in the grafted tobacco is not a result of the transfer of anabasine from the stock into the scion, but is due to a complete modification of the biochemical process of alkaloid formation in the scion which occurred owing to a specific influence of the stock.

4. The study has shown an exceptionally strong influence of stock upon scion which opens great possibilities in the intervention into the chemical composition of the plant and of production of grafted plants with new chemical composition.

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BIOCHEMISTRY

ON THE POSSIBLE RELATION BETWEEN THE ASYMMETRY OF THE ORGANISM AND OPTICAL ACTIVITY OF THE SUBSTANCES IT IS COMPOSED OF. I. AMINOACIDS FROM THE CONCHIOLIN OF SHELLS WITH RIGHT AND LEFT DIRECTION OF THE WHORL

By A. KIESEL, E. EFIMOCHKINA and J. RALL

(Communicated by W. I. Vernadsky, Member of the Academy, 3. VIII. 1939)

It seemed of interest to verify the opinion repeatedly advanced by W. I. Vernadsky as to the possible existence of a connexion between the morphological asymmetry of organisms and the optical asymmetry of the compounds found in the former, using such representatives of the organized world which exist in two modifications, mutually opposite by their morphological form.

Some molluscs having conches with whorls going in one direction with certain species, and in an opposite direction with other ones, are examples of such forms. It is interesting to mention here that one of these asymmetric modifications, as may be seen from numerous observations, shows prevalence over the other in its wider range of distribution, frequency and number of individuals, as well as in its evidently better accomodation to the existing life conditions.

When selecting in the organism a chemical body for which optical activity must be a most characteristic feature, it seemed quite natural to chose proteins. As two types of proteins easy to separate and different by their biological significance and their physiological rôle are found in molluscs, i. e. proteins of the skeleton and proteins of the active tissue, it was proposed to study both types of proteins.

A paper by Kögl and Erxleben (1) on the disturbance of the stereoisomeric specificity in the proteins of cancer tissues in respect of the molecules of aminoacids they are composed of, which appeared when this investigation was in progress, considerably increased the importance of this study.

The main subject of our investigation were modifications of the mollusc *Fruticicola lantzi* Landh. showing right or left volution. Both modifications were collected in the region of Alma-Ata and obtained through G. F. Gause. Besides, two other species of molluscs, collected in the Moscow region, have been investigated, namely, *Limnaea stagnalis* L. with right volution, and *Aplexa hypnorum* L. with left one. It stands to reason that the comparison of the two latter forms could not have the same importance as that of the two former modifications of one and the same species.

For the present investigation conchiolin was prepared as thin brown pellicles, according to the procedure coinciding in the main with the method described by G. Wetzel (2).

All attempts to obtain solutions of these proteins that would be sufficiently clear and transparent for polarimetrical determinations, proved a failure. We even used such vigorous solvents as hot 20% hydrochloric acid, but we refrained naturally from alkaline solvents fearing the racemisation of the protein. Our failure made us give up the determination of the optical activity of the proteins and induced us instead to pass over to an investigation of the optical activity of products of the hydrolysis of the protein. Such products were selected that could be easily obtained through fractionation of the hydrolysate. This restriction had to be introduced because of the relatively small amount of conchiolin that had been obtained from the material at hand.

Limnaea stagnalis L. (right form)— 11.1 g from 4800 molluscs
Fruticicola lantzi Landh. (» »)— 7.22 g » 1497 g of conches
» » » (left »)— 4.86 g
Aplexa hypnorum L. (» »)— 4.03 g

The yield of aminoacids was, moreover, considerably decreased by the fact that the conchiolin preparations were far from being pure, as it may be seen from the nitrogen content quoted below and from the large amount of humic constituents, that formed considerable precipitates after the hydrolysis which was carried out by means of 25% sulphuric acid during 16 hours.

Conchiolin	Nitrogen, %	Insoluble humines, %	Nitrogen in humines, %
Limnaea	13.10	12.70	1.51
Fruticicola (d)	12.68	10.22	1.66
» (l)	9.56	19.87	1.24
Aplexa	12.13	8.13	2.32

The fractionation of aminoacids was carried out through the precipitation of the basic products with phosphotungstic acid with a subsequent separation as Ag-compounds ([3]). Then tyrosine and leucine were isolatad through crystallization.

The determination of specific rotations was carried out in case of hexonic bases in an aqueous solution, and in the case of tyrosine in 4% and of leucine in 24% hydrochloric acid. For hexonic bases samples were determined by the nitrogen content in the corresponding non-crystalline and rather strongly coloured fractions. Samples of tyrosine and leucine were taken after repeated crystallization, so far as it was allowed by the amount of the product. The direct readings of the angle of rotation were within the limits of 0.18—0.86°. The majority of readings were near 0.3°. The small dimension of the angle was caused by the smallness of the samples, as well as by the limitations of visibility in coloured solutions. The size of the deviation from the usual norm of specific rotation was certainly affected by certain imperfectness of the fractionation itself, since the presence of some admixtures different by their optical activity could not have been excluded.

The data of the $[\alpha]_D^{20}$ of aminoacids from conchiolins are given in the following table (p. 483).

Notwithstanding the rather considerable deviations of the value of $[\alpha]_D^{20}$ from the norm, this being explained in the way expressed above, we see no indication that the asymmetry of the form is in any way connected with the optical isomerism of amino-acids, out of which the protein molecule is built. However, in the present case it is only the auxiliary, skeleton protein that has been investigated. A necessary continuation will be the study

	The $[\alpha]_D^{20}$ that ought to be	*Limnaea stagnalis* right form	*Fruticicola lantzi* Landh.		*Aplexa hypnorum* L. left
			right	left	
Arginine	+26.5	+25.4	+36.0	+25.8	+25.8
Histidine	−39.7	−49.7	−34.0	−41.7	−47.7
Lysine	+15.3	+19.5	+21.1	+20.3	+18.0
Tyrosine	−16.2	−16.1	−15.9	−19.0	−15.7
Leucine	+18.9	+24.5	+25.1	+22.1	+17.0

of the constitutional protein of the organism. This has been accomplished as far as possible, and the results will appear in another paper in the nearest future.

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CHEMISTRY

MODELS OF PROTEIN MOLECULES

By D. L. TALMUD, Corresponding Member of the Academy

In establishing the structure of protein molecules, each of which contains many thousands of atoms, chemistry has met with insuperable difficulties. It is natural therefore that different models of protein molecules have been proposed which explained in a hypothetical way only the most characteristic properties of proteins. The first and perhaps the most successful was the model of silk fibroin proposed by Meyer and Mark(1). This model gave a satisfactory interpretation of the X-ray diagram of silk fibroin. But even in this simplest case Meyer and Mark make the arbitrary and chemically unfounded assumption that the molecules of silk fibroin consist of polypeptid chains with but two alternating aminoacids: glycine and alanine. Other aminoacids, the presence of which in silk fibroin to the amount of nearly 35% (2) has been shown analytically, are contained, according to Meyer and Mark, in the amorphous protein, filling the space between the crystallites. The absence of side chains in glycine and alanine does not complicate the shape of the polypeptid backbone, and the identity periods which are observed in the X-ray diagrams are in good agreement with the dimensions of the aminoacids forming the chain.

The protein fibres of keratine, collagen, lyosine and others have a much more complicated composition than silk fibroin. Models of these molecules which have been constructed by Astbury (3) for the explanation of their physical-mechanical properties are based on still more hypothetical assumptions. All the models of Astbury imply the possibility of a regular folding of the polypeptid chains, transforming the molecular thread into a plane. Although these models lead to a successful interpretation of the X-ray diagrams of extended keratine, they give rise to a number of objections. The hexagons which are formed by the folding of the polypeptid chain consist of two aminoacids and leave but very little room for side chains. Even in the most extended polypeptid chain the side chains of more or less complex aminoacids must feel rather «tight». Let us consider, for example, a portion of a polypeptid chain, consisting of tryptophane, cystine and tyrosine (Fig. 1). Still more objectionable is Astbury's assumption about the rôle of hydrogen bond in a transition of the elements of the folded chain from the lactam to the lactim form.

Very similar in certain respects are the models of globular proteins, proposed by Wrinch(4). Starting with the «cyclol» hypothesis of Frank(5) on the hydrogen bond between the carbonyl and the imine groups in the polypeptid chain, Wrinch develops her conceptions on the branching of the aminoacid bonds in a plane and on the closing of planes into space with formation of

polyhedra of a certain shape. The cyclol hypothesis has met with a number of serious, perhaps crushing objections([6]). In contradistinction to the models of fibrous proteins, Wrinch's models attempted to explain the fundamental properties of globular proteins: the discreteness of molecular weights and the approximately spherical shape. An attempt at a construction of a unified model of fibrous and globular proteins must take into account these most important properties of globular proteins. It is therefore impossible to agree with Pauling([6]) who attempts to «explain» the discreteness of the molecular weights of globular proteins by a «natural selection» of polypeptid chains of a definite length in the process of evolution of organisms.

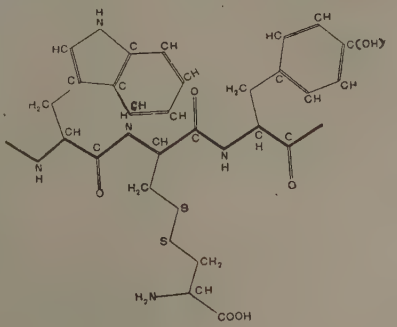

Fig. 1.

The general drawback of all the models of protein molecules suggested heterofore is the actual overlooking of side chains in the aminoacid residues. A separate consideration of the structure of the polypeptid backbone and of the structure of the lattice of side chains can perhaps be commended didactically; it is, however, beyond doubt that the structure of the polypeptid backbone is determined to a certain extent by the structure of the lattice of side chains and vice versa. The results of fundamental researches by Bergmann and his co-workers([7]) on the enzymatic splitting and synthesis of artificial substrates show very persuasively the decisive rôle played by the structure of the side chains, their configuration and relative position. Now the biochemical properties of proteins are not taken into account by the existing models.

Out of the different biochemical properties of proteins which must be explained by the models of the globular proteins, the following are especially important: a) all the α-aminoacids extracted from proteins have the same (left) optical configuration; b) the artificial substrates of Bergmann, which are split up by proteinases, must be built up from *l*-aminoacids only, while the substrates split up by peptidases—sometimes from both *d*- and *l*-aminoacids; c) the enzymatic synthesis of the so-called plastein([8]) shows that the primary units, from which a globular molecule is apparently built up and which possess protease properties, have a molecular weight somewhat less than 1000([9]).

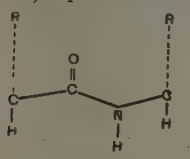

Fig. 2.

The new model of globular protein molecules which we advance here is but a first attempt at an adequate estimate of the polypeptid backbone and of the side chain lattice in the structure of protein. The fundamental feature of the new model consists in accounting for the effects which are due to the mutual action of the side chains. This mutual action amounts to 2 kcal/mol. CH_2 or about 600 kcal/mol. of the protein with a molecular weight of 35 000. Only in the case of silk fibroin it is apparently possible to neglect this mutual action. If one takes into account that the natural synthesis of protein molecules occurs in aqueous solution, the mutual action of the side chains of condensing aminoacids leads to an accumulation of side chains in one plane with respect to the polypeptid backbone. This is equivalent to a curling of the polypeptid chain into a ring, all the links of which have side chains on the same side of its plane. For purely geometrical reasons the

formation of such a ring is possible in that case only when all the aminoacid residues contained in it have the same optical configuration. From a mixture of left and right aminoacid residues it is impossible to build up a polypeptid chain in the shape of closed ring with all the side chains lying on the same side of the plane of the ring. The minimum number of aminoacids which can make a ring-shaped polypeptid chain is equal to six. Such a chain will be denoted in the sequel as a ring chain. Such a hexagonal ring chain is a space structure; its projection on the plane has a diameter of about 6.3Å, the length of the side being 3.82 Å [the distance C — C = 1.54 Å, C—N=1.40Å ([10])].

Fig. 3.

Along with the side chains the ring chain must be similar to a hexagonal prism, with a height equal to the average length of the side chains and a cross-section of the following form (Fig. 2).

The ring chains can be considered as primary units serving for the construction of the globular protein molecule. The molecular weight of a ring chain must lie between 693 and 744([11]), if the average molecular weight of the aminoacid residue lies between 115.5 (haemoglobin) and 124 (egg albumin). This agrees in the order of magnitude with the molecular weight of plastein.

The ring chains can combine with each other into a complex molecule by the bonds of three different kinds: a) electrostatical mutual action between the feebly polar peptid bonds, b) mutual action of the side chains and c) a reaction of additional condensation. The a) and b) bonds must, however, be rejected, for the ionic bond is greatly weakened in an aqueous solution, and the mutual action between the side chains could not lead to a homodisperse solution of molecules. There remains, accordingly, but the additional condensation. Two ring chains turned towards each other with opposite faces can participate in the condensation reaction, if one of the peptid bonds is in an isomeric form (Fig. 3).

Fig. 4.

The angle between the planes of the linked ring chains must be a tetrahedral one. Owing to the subsidiary condensation reaction, the ring chains can combine with each other forming long chains (which in their turn can be closed into a ring) and planes. As a result of the subsidiary condensation, however, the ring chains can build up polyhedra, too. The simplest polyhedron consisting of equilateral hexagonal faces intersecting under a tetrahedral angle is a combination of a cube with an octahedron, consisting of eight hexagonal faces and of six tetragonal (in our case hollow ones) (Fig. 4). Such a polyhedron consists of 48 aminoacid residues, its molecular weight being equal to 5500—6000. Through a combination of such polyhedra it is easy to obtain molecules with all the molecular weights which have been observed by Svedberg.

The model proposed meets all the requirements. The formation of a ring chain, in which all the side chains are situated on the same side of the ring plane, gives a satisfactory explanation of the fact that all the aminoacids of natural origin belong to the same optical configuration. The reason for this configuration to be a left one is apparently connected with the genesis of aminoacids from sugars or related products. The Walden inversion could lead under certain conditions to the formation of left aminoacids from both right and left sugars.

The difference between the proteinases and peptidases found by Bergmann in the enzymatic splitting of artificial substrates also permits of a simple explanation. The enzymatic hydrolysis is certainly similar to hydrolysis under the catalytic action of acids and bases, being complicated by the presence of zwitterions and by definite steric conditions as to the relative position of the side chains of the enzyme and those of the substrate. If the side chains of the enzyme which contain free carboxyl and amine groups, giving an intermediate compound with the substrate, are situated in different parts of the ring chain, the substrate must consist of *l*-aminoacid residues only. If, on the other hand, the groups of the enzyme which further the hydrolysis are connected with the same side chain, then the artifical substrate can consist both of *d*- and *l*-aminoacid residues.

It is finally possible to give a simple explanation of the unique phenomenon of denaturation. Denaturation consists at least partly in a transition of the «native» protein with a small activation energy (about 1 kcal/mol. aminoacid) into a new state, in which the presence of polypeptid chains has been firmly established([13]). Denaturation, in our opinion, can be connected with an easily proceeding racemization. The formation of aminoacid residues of a different optical configuration is not compatible with the existence of a ring chain.

The formation of globular molecules from primary polyhedra does not exclude the hypothesis of intraglobular reactions ([13]). This hypothesis is only simplified, for it is sufficient to assume the intraglobular formation of a single ring chain (and not of a whole protein molecule) in order to give an acceptable scheme of the chemical reproduction of protein.

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CHEMISTRY

SYNTHESIS OF β-HYDROXYVALINE AND OF β-HYDROXY-α-(N-METHYL)-AMINO-(n)-BUTYRIC ACID

By M. A. PROKOFIEV and M. M. BOTVINNIK

(Communicated by N. D. Zelinsky, Member of the Academy, 10. X. 1939)

The hydroxyaminoacids belong to those aminoacids from proteins that are least known. Lately investigators are paying more and more attention to these substances, particularly because of there being indications concerning their rôle in the living organism.

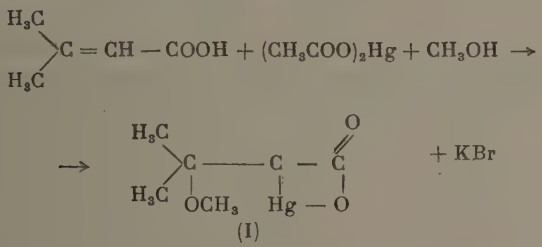
Owing to a proposal of N. D. Zelinsky, we have undertaken a series of investigations on the synthesis of hydroxyaminoacids and of their derivatives. With the exception of tyrosine and serine until lately hydroxyaminoacids were accessible rather with difficulty*. The simplest synthetical method starting from α-β-unsaturated acids through the corresponding hydroxyhalogenoacids proved to be unsuitable, since as a result of this reaction the formation of a mixture of the β-hydroxy-α-amino- and of the β-amino-α-hydroxyacid took place, and because it was impossible to separate this mixture into components(1). In 1922 Schrauth and Geller(2) have found that the esters of α-β-unsaturated acids react in an alcohol medium with mercuric acetate with the formation of β-R-hydroxy-α-mercury derivatives. In these compounds mercury can be easily substituted by a halogen with the formation of a β-R-hydroxy-α-halogenoacid which by means of a subsequent amination and hydrolysis is transformed into a β-hydroxy-α-aminoacid. By this method these authors have synthetized hydroxyvaline. West and Carter(3) have shown that free α-β-unsaturated acids, such as for instance crotonic acid, react in the same way, and obtained from crotonic acid threonine. Later, West, Crummel and Carter(4) have found that a β-R-hydroxy-α-bromoacid is formed without corresponding isomerides through the bromination of an α-β-unsaturated acid in an alcohol solution in the presence of silver nitrate. Using this method, they also obtained threonine, but with a poorer yield.

In the present paper we have established that hydroxyvaline can be obtained as well according to the method of West and Carter directly from dimethylacrylic acid. Besides, we have obtained a new aminoacid, not described in literature, β-hydroxy-α-(N-methyl)-amino-(n)-butyric acid.

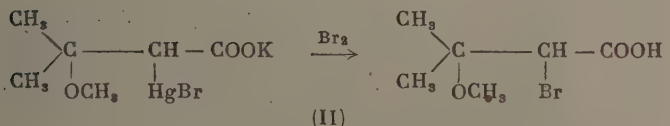
The synthesis of hydroxyvaline consisted of the following steps: α-β-dimethylacrylic acid was treated with mercuric acetate in a methyl alcohol solu-

* A detailed list of the literature concerned see Abderhalden and Heyns, Ber., 67, 530 (1934); also Knoop, Ditt, Hecksteden, Maier, Merz and Härle, ZS. Physiol. Chem., 239, 30 (1936); Adkins and Reeve, J. Am. Chem. Soc., 60, 1328 (1938).

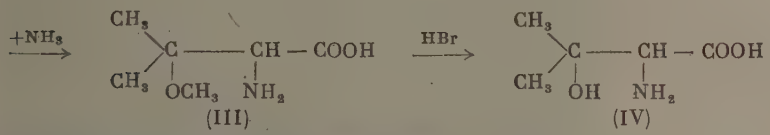
tion, with the formation of a β-methoxy-α-anhydro-mercuro-derivative(I). The latter under the influence of KBr and Br_2 was converted into a β-methoxy-α-bromoisovaleric acid(II) which after amination gave a β-methoxy-α-aminoacid (III). Through hydrolysis by means of hydrobromic acid β-hydroxy-α-aminoisovaleric acid was obtained:



(I)



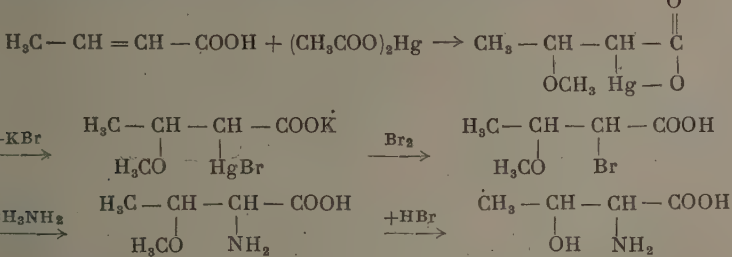
(II)



(III) (IV)

The yield of hydroxyvaline amounted to 21.6%. Hydroxyvaline is a white crystalline matter with a sweet taste. Its melting point (with decomposition) is 218°. Nitrogen content: calculated 10.53%, found 10.52; 10.48%. Therefore dimethylacrylic acid, as well as crotonic acid, gives only an α-mercuri-derivative.

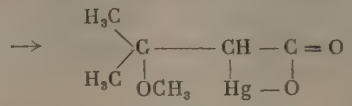
β-Hydroxy-α-(N-methyl)-amino-(n)-butyric acid was obtained with a yield of 20.4% in a similar manner, but starting from crotonic acid. The amination of β-methoxy-α-bromo-(n)-butyric acid was carried out by means of an aqueous solution of methylamine in sealed tubes.



β-Hydroxy-α-(N-methyl)-amino-(n)-butyric acid is a white powder that crystallizes from absolute alcohol in small laminae and has a weak sweet taste.It is easily soluble in water, poorly in alcohol, insoluble in acetone and ether. Its melting point in a sealed tube is 234—235° with decomposition. Analysis: calculated for $C_5H_{11}O_3N$: C=45.08%, H=8.33%, N=10.53%; found: C=45.29—45.19%, H=8.40—8.41%, N=10.52—10.54%.

I. Synthesis of Hydroxyvaline. The initial substance was dimethylacrylic acid, obtained from mesityl oxide according to the method of Barbier and Leser(5), melting point 70°.

1. β-Methoxy-α-anhydro-mercuri-isovaleric Acid



In order to find the best conditions for this reaction, a series of experiments was arranged, in which the influence of temperature and of the molar ratio of dimethylacrylic acid and mercuric acetate was determined. The results of these experiments are given in the table.

Dependence of the Yield of β-methoxy-α-anhydro-mercuri-isovaleric Acid on Conditions of the Experiment

Exp. No.	Conditions of experiment	Ratio of dimethylacrylic acid to mercuric acetate	Yield of β-methoxy-α-anhydro-mercuri-isovaleric acid, %
1	Boiling methyl alcohol	1 : 1	64
2	18°	1 : 1	73
3	18°	1 : 2	0
4	18°	1 : 0.5	35.05

It may be seen from these experiments that the maximum yield is obtained when the reaction is carried at room temperature with a molar ratio of the reagents. Accordingly, the synthesis of methoxy-α-anhydro-mercuri-isovaleric acid was carried out in the following way.

To a solution of 60 g (1 mole) of dimethylacrylic acid in 900 cm³ of methyl alcohol, 183.6 g (1 mole) of mercuric acetate were added. The mixture was shaken vigorously and in a few minutes all the mercuric acetate passed into solution. After standing for 2—3 hours at room temperature, the separation of a white crystalline precipitate began and was completed after 48 hours. The mother liquid was coloured dark-red, the crystals were filtered off, carefully washed with methyl alcohol and dried in a vacuum-desiccator over sulphuric acid. The product was insoluble in water and in ordinary organic solvents. Its melting point in a sealed tube was 159—160° with decomposition. The content of mercury was determined according to Rupp and Noll:

Calculated for $C_6H_{10}O_3Hg$: Hg→60.66%.

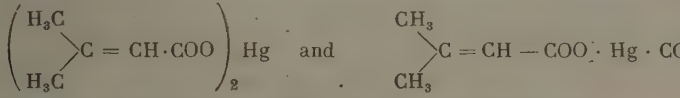
Found: 60.16;60.33%.

The yield was 140 g,73% of the theoretical amount.

As it was mentioned above, the mother liquid of the mercuri-derivative was coloured dark-red. The less the yield of the normal addition product, the more intensive the colour. When the mother liquid was evaporated dry and the residue washed with ether, it was possible to obtain dark-red crystals insoluble in ether, toluene, xylene, water and in a solution of potassium bromide, and on the contrary, well soluble in methyl and ethyl alcohols, pyridine, chloroform and acetone. When dissolved in glacial acetic acid and diluted hydrochloric acid, the formation of a white crystalline powder took place.

A test on the double bond with potassium permanganate and bromine water gave positive results (the colour of the product itself disappeared also).

These crystals have not been studied more completely. The possibility is not excluded that they are a mixture of two mercury salts:



which are not described in literature, as far as we know.

2. α-Bromo-β-methoxy-isovaleric Acid. 185.3 g (1/2 mole) of the compound (I) were dissolved in 600 cm³ of water containing 119 g of potassium bromide (1 mole). There separated a small amount of a dark precipitate which was filtered off. To this solution a mixture of 80 g bromine (1/2 mole), 90 g KBr and 150 cm³ of water was added gradually under mechanical stirring and cooling with ice. The bromination lasted for about 2 hours, after which the reaction mixture was extracted with 100 cm³ of ether to eliminate admixtures, acidifed with 100 cm³ of 48% hydrobromic acid, and again extracted with 1000 cm³ of ether (in 4 portions). The ether extracts were dried with sodium sulphate. After the distillation of ether, there remained in the flask a slightly coloured thick oil, raw α-bromo-β-methoxy-isovaleric acid. The yield was 92.7 g or 87.9%. The pure acid, according to Schrauth and Geller, forms crystals melting at 77°. But, according to West and Carter, the oil obtained after bromination is sufficiently pure for further reactions.

3. α-Amino-β-methoxy-isovaleric Acid. 50 g of technical β-methoxy-α-bromo-isovaleric acid were mixed with 250 cm³ of 25% ammonium hydroxide solution and heated for 2 hours at 100° under pressure. Then the solution was evaporated under reduced pressure until dry. The main portion of the light yellow crystalline mixture of α-amino-β-methoxy-isovaleric acid and ammonium bromide was treated as described below for the preparation of hydroxyvaline. A small portion of the mixture was treated with hot absolute alcohol in order to isolate pure α-amino-β-methoxy-isovaleric acid. The acid was recrystallized twice from 80% alcohol. Its melting point was 253—254° with decomposition. According to Schrauth and Geller, this acid has a melting point 250—260° with decomposition.

Nitrogen content: calculated 9.52%, found 9.60%.

4. Hydroxyvaline. The mixture of α-amino-β-methoxy-isovaleric acid and ammonium bromide was boiled for 1 hour with a 10-fold amount by weight of 48% hydrobromic acid. In order to eliminate the main amount of HBr, the solution was evaporated several times with water under reduced pressure. Ammonium bromide and resinous matters that fall out during the evaporation were filtered off. The residue was dissolved in water, ammonium hydroxide was added to a definite alkali reaction, and it was again evaporated under reduced pressure until dry.

In order to isolate pure hydroxyvaline, the residue was extracted several times with absolute and 96% alcohol in a Soxlet extraction apparatus. The yield was 10.72 g or 21.59%, reckoning on dimethylacrylic acid. The product had a melting point 218° with decomposition. This agrees with the data of Schrauth and Geller.

Nitrogen content: calculated 10.53%, found 10.48; 10.52%.

Hydroxyvaline has a sweet taste. It is readily soluble in water and poorly in alcohol.

II. Synthesis of β-hydroxy-α-(N-methyl)-amino-(n)-butyric Acid. As initial product crotonic acid was used. The latter was obtained through the condensation of melonic acid with acetaldehyde in the presence of pyridine according to the method of Scheibler and Magasanik(7). Melting point 71°.

1. α-Bromo-β-methoxy-n-butyric Acid. This acid was obtained from crotonic acid using the method of West and Carter. From 200 g of crotonic acid when treated with mercuric acetate in a methyl alcohol solution, 689 g of β-methoxy-α-anhydro-mercuri-derivative were obtained. Yield 80%. When the latter was treated with potassium bromide and bromine, 325 g of technical β-methoxy-α-bromo-(n)-butyric acid were obtained. Yield 90%. According to West and Carter, the acid is sufficiently pure for further synthesis.

2. β-Hydroxy-α-(N-methyl)-amino(n)-butyric Acid. 63.5 g of β-methoxy-α-bromo-butyric acid were treated in three portions with a ten-fold amount of 40% aqueous solution of methylamine. The mixture was heated for 5 hours at 100° under pressure. The duration of the heating period was found out by means of preliminary experiments, in which the ion of bromine was titrated according to Volhard. The reaction mixture was evaporated several times with water under reduced pressure in order to eliminate the excess of methylamine. There formed a dark and very thick mass which after standing for 48 hours under a layer of acetone partly crystallized. In order to eliminate the methoxyl, the mixture was hydrolyzed through boiling for $1^1/_2$ hours with 160 cm³ of 48% hydrobromic acid. The excess of the latter was eliminated through a manifold evaporation with water under reduced pressure. The residue—a thick and dark syrupy liquid—consisted of a mixture of the aminoacid with ammonium bromide. The syrup was dissolved in water and subsequently treated with barium hydroxide, sulphuric acid, silver oxide and hydrogen sulphide. After evaporation under reduced pressure 27 g of a dark thick residue were obtained, out of which after the addition of absolute alcohol the aminoacid crystallized in small white laminae. It was treated twice with absolute alcohol and recrystallized from 96% alcohol.

β-Hydroxy-α-(N-methyl)-amino-(n)-butyric acid has a feeble sweet taste. Its melting point in a sealed tube is 234—235°. At this temperature it turns over into a light-brown oil with the odour of an amine and it does not crystallize. It is well soluble in water, poorly in alcohol, insoluble in acetone and ethers. Yield 12.1 g or 20.4% reckoning on crotonic acid.

Analysis: calculated for $C_5H_{11}O_3N$: C=45.08%, H=8.33%, N=10.53%. Found C=45.29; 45.19%; H=8.40; 8.41%; N=10.52; 10.54%.

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GEOCHEMISTRY

ON THE GENESIS OF THE TAMDA EMERY DEPOSITS

By A. F. SOSEDKO

(Communicated by A. E. Fersman, Member of the Academy, 5. X. 1939)

As early as in 1932 several emery deposits occurring among marbles were detected in the Tamda massif in the central part of the Kyzyl-Kumy desert (the Kara-Kalpak Autonomous Republic). The reconnaissant character of the search did not allow at the time to closely approach the problem of the genesis of these deposits, and from their analogy with other deposits they were referred to endogene deposits formed as a result of desilication of a pegmatitic melt (1).

In 1938 the Kara-Kalpak expedition of the Geological Institute of the Scientific Committee under the Council of People's Commissaries of the Uzbekistan organized a more detailed study of the Tamda deposits. As a result of this study there were made conclusions which are of great scientific interest and practical importance. A brief exposition of these is the subject of the present paper.

The region of the deposits is composed of a complex of Paleozoic rocks subdivided into a number of beds. At the base of the section are lying quartz-sericite schists. These are overlain by marble beds about 700 m thick which may be subdivided into several series. The lower part consists of arenaceous reddish marbles; higher up they pass into a series of black laminated marbles. The latter are overlain by a thick series of massive non-laminated light-coloured marbles; higher up follows a series of the upper black laminated marbles about 100 m thick. The marble beds pass into the upper beds of siliceous argillaceous shales with bands of a conglomerate.

The lower schistose beds are not characterized faunistically, they are referred presumedly to the Upper Silurian; the marble beds and the upper shistose beds contain fauna of the Upper Silurian.

The rocks are crumpled into folds of a latitudinal strike. The majority of deposits are confined to the Adzheriktinsk at the next southern Aktauss anticline. The structure of the latter is of interest. This is a large dome-like uplift with a complicated construction of the limbs. A number of folds of the second order are observed, owing to which the surface of the limbs assumes its ruffled aspect. The western part of the Aktauss anticline is complicated by the penetration of a granite intrusion; beside the disturbances, breaks and faults are observed along the strike of the rocks.

Of igneous rocks granite, ultrabasic rocks and different vein rocks are observed here. The granite is red and occupies an area of about 30 km^2. The contact with marbles is active, the contact plane mostly follows concordantly

the strike of the rocks. Of ultrabasic rocks chiefly serpentines are encountered, passing at the margins to a hornblende gabbro. They break through the overlying schists, and their outcrops appear at a distance of 0.5 km from those of the marble. Of vein rocks lamprophyre veins (spessartites, malachites, etc.) are predominating. They intersect both marbles and shists; much rarer are quartz porphyres.

The emery deposits are confined to the upper part of the Upper Silurian marbles. In the western deposits they are clearly seen to occur in the light-coloured marble beds at their boundary with the upper black marbles. The emery occurs in the shape of lenses of different size, from several centimeters to 50 m, as measured along the long axis. Small lenses from 1 to 2 m prevail. A feature peculiar to these deposits is that the lenses are confined to a thin (up to 10 m in thickness) horizon. Along the strike, however, the ore-bearing horizon may be traced occasionally for hundreds of meters. In the Chinghildinsk deposit it may be observed that the character of the ore bodies does not change either with the depth, or with the dip, or along the strike, though the lenses along the vertical are traced for 100 m, and along the dip for 300 m. It does not change near the vein rocks and tectonical disturbances either. The emery lenses are always arranged in such a way that the long axis follows the strike of the rocks, and not a single lens was encountered which would fill up the breaks in the marbles. On the contrary, it may be observed that the marble layers seem to flow around the ore lens. On taken up ore lenses one may see that their bottom walls rest upon an uneven clearly corroded surface, while the marginal contact of the hanging wall is more or less even. The structure of the ore bodies shows neither zonality in the arrangement of individual ore types, nor any regularity in the arrangement of definite ore types with regard to the marginal contacts.

From its composition and structure the ore is various. It presents a fine-grained rock consisting of a mineral aggregate from 0.01 to 0.1 mm in size, rarely larger.

The mineralogy of the ore bodies is insufficiently studied. The presence is proved of the following minerals which are listed here in order of their abundance: pyrophyllite, corundum, margarite, an amorphous mineral not identified; hydrargillite, rutile, chlorite, tremolite, brown ironstone, biotite, andalusite, kaolinite, diaspore are encountered less frequently; quite rare are quartz and pyrite. Diaspore, hydrargillite, brown ironstone, quartz are secondary minerals, that are filling up partings in the ground ore-mass.

The structure of the ore is highly interesting. In the Chinghildinsk deposit located 2 km on a straight line from the granite massif, a «yellow» ore is predominant. Under the microscope it proves to consist of a ground-mass of minute amorphous minerals non-reacting to passing light, enclosing sometimes round, sometimes ellipsoidal accumulations of anisotropic minerals 0.1—1 mm in size. These accumulations are stretched out with their long axis in the direction of the lamination observed in thin-section. The accumulations consist of minute grains and resemble caviar.

The minerals in the accumulations are chiefly corundum and pyrophyllite (?). In some cases a concentric botryoidal structure is observed. Such a structure may be called only oolitic. The structure of the ore predominating in the Asche-bulak deposit located directly in the vicinity of the granite, is different, though by their chemical composition the ores closely resemble each other. The ore here is holocrystalline, no amorphous substance is observed. Corundum is encountered here in coarse round grains from 2—3 to 0.1 mm in diameter; usually, the grain consists of one individual, in some grains

a clear relict oolitic structure is observed. Fine corundum grains are usually idiomorphous. Among the corundum grains margarite is enclosed.

In comparing the structure of the above ores, the conclusion may be made that they were originally quite identical both as to their mineralogical composition and structure. As a result of temperature influences upon the granite intrusions, metamorphization of the ore took place. In ore bodies located further from the granite metamorphization was only slight; while in those lying near the granite the thermal effect led to a deeper metamorphization manifested in a complete recrystallization of the initial substance. The metamorphism here took place not at the expense of an alteration of the chemical composition, since neither losses nor addition of elements have been observed, but only produced a rearrangement of molecules.

A study of the chemical composition by means of both chemical and spectral analyses showed that from the character of variation of the content of individual elements the ore of the Tamda deposits closely approach bauxite ores. Spectral analysis showed the presence of the same rarely encountered elements which are present in bauxites, and did not show any elements which would be due to endogene processes.

All of these cumulative data show that there are no facts bearing evidence in favour of the origin of the Tamda emery from a pegmatite melt by way of desilication of the latter. On the contrary, it is quite clear and convincing that they are formed at the expense of metamorphization of sedimentary rocks rich in aluminium: bauxites, allites, etc.

It is evident that not only the Tamda deposits, but also the numerous emery deposits known in the Nuratinsk mountains, the Turkestan and Alai ranges have been formed in this way.

According to the sedimentary metamorphic theory of the formation of emeries in Middle Asia, one should expect to encounter bauxite occurrences in the slightly metamorphized Upper Silurian limestones. However, up to the present they have not been found in these. Moreover, one should expect the presence of new emery deposits in places where these limestones have been subjected to intense metamorphization. It is to be noted that such facts in favour of the sedimentary metamorphic origin of emery in marbles have so far not been described in literature.

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MINERALOGY

CONTRIBUTION TO THE PROBLEM OF THE DEPENDENCE OF WEATHERING OF MINERALS UPON CLIMATIC CONDITIONS

By P. ZEMIATCHENSKY, Corresponding Member of the Academy

Weathering of Muscovite. Mica in the form of both biotite and muscovite which enter into the composition of local granites, gneisses and micaceous schists, is widely spread in the region of the Chibina mountain range and in general on the Kola Peninsula and in Karelia. Moreover, muscovite forms occasionally large segregations in pegmatite veins which are of considerable industrial importance.

The results of weathering are particularly illustrative in iron containing micas and especially in biotite. The change in this case becomes manifest through the appearance of a brown hue. The dark grey colour of fresh mica gradually becomes yellowish-brown.

As material for our investigation on the weathering of muscovite, specimens obtained from the Tchupa district (Karelia) were used, as well as samples collected by the author in the environs of the town Viatka among the ruins of an ancient church, in which mica served instead of glass. This material had probably as its country of origin also Karelia, where the extraction of mica was practiced since olden times. The specimens obtained from the environs of Viatka, apart from the fact of their originating from a district far remote from Karelia, present outstanding interest also because they permit to judge of the rate of weathering of muscovite. The mineralogical character of the muscovite of Karelia and its industrial value have been described by I. I. Ginsburg (1).

From the analysis of mica out of native deposits as given by Ginsburg it will be apparent that the muscovite of Karelia show the following fluctuations of the principal components (in %):

SiO_2	45.64—47.05	Na_2O	0.85—1.01
Al_2O_3	30.50—34.64	Loss upon ignition	2.57—4.51
Fe_2O_3	1.81— 5.64	Hygroscop. water	0.01—0.24
K_2O	10.18—10.36		

Weathering of Tchupa Muscovite. The specimen of Tchupa muscovite which was at the author's disposal consisted of large laminae which were entirely transparent in their middle portion; colourless—in the thinner layers; and smoke-coloured—in the thicker parts. The laminae are flexible and elastic. At its periphery, the muscovite assumes an ochre-yellow hue and becomes turbid and brittle, with a very gradual transition to the parts of the micaceous lamina left intact. Under the microscope it is possible to see clearly how fresh muscovite undergoes gradual change in course

of its weathering. The transparent and colourless laminae of mica grow turbid, the turbidity extending from the periphery inwards and suffering a gradual decline in intensity. The spreading of the turbidity is irregular, being patterned in the shape of tongues which sometimes penetrate deep into the body of the mica lamina. As the turbidity increases, the colour varies, too, the change proceeding in the direction of yellow. This is due to the formation of free iron hydroxide which, as shown by analyses, is always available in the muscovite of Karelia.

In polarized light bi-axiality remains the same as in the non-weathered portion of the micaceous lamina, with the only difference, that the hyperboles now present a diffuse and dim appearance. Weathering starts off with splitting of a muscovite scale along the cleavage planes, where the earthy products of weathering become accumulated. Besides this, a crushing of the micaceous lamina into smaller parts is also observable.

Under the microscope, the smallest scales of muscovite seem as it were built up of dots, so fine-grained are they, this accounting for the turbid appearance. In some places disintegration of the small scales into separate transparent very fine grains is noticeable. Evidently, along with chemical changes, dispersion of muscovite laminae takes place in an increasing measure, which, most probably, leads in the last account to the formation of a sol; the latter in the form of a pseudosolution is liable to be removed, leaving behind but the coarser particles of muscovite. Thus, the components of muscovite are driven away, there remaining on the spot only the iron hydroxide.

To investigate the weathering of mica from a chemical angle, the following method was resorted to: in the first place a selection was made of such specimens, in which the weathering became manifest through a change in transparency, through more intensive colouring (due to the hydroxide of iron standing out), and also through splitting. Such samples were now divided with the help of a knife into the finest possible flakes which were thereupon kneaded by hand; in this process the most weathered parts were easily crumbled off and separated from the less weathered parts of the micaceous flakes. By sifting through a mesh of 0.25 mm the finer parts were separated from the coarser ones and then ground to the consistency of fine powder. These parts represented the most weathered portion of the muscovite.

The flakes which had remained uncrushed after kneading now underwent a slight grinding in an agate mortar. In course of this, those particles became detached from the flakes which were not held as firmly as the less altered part of the mica flakes. The separated particles, just as in the first case, were next subjected to sifting through a 0.25 mm sieve, being then ground to the consistency of fine powder. In this way, a material was obtained, in which the different stages of the weathering of mica found their expression. Finally, the remaining scarcely friable flakes represented the mica which was either not at all, or but slightly exposed to weathering.

Chemical Composition and Character of Muscovite at Different Stages of Weathering. In order to provide a general characteristic, the total chemical composition of a non-weathered, as well as a weathered muscovite was in the very first place determined. The chemical composition of the unaltered muscovite and that of its weathered portion is given in Table 1.

For establishing the nature of the weathering products of muscovite, the method of treating the material with different reagents was used. We employed a 5% soda solution and a 10% HCl solution. For analysis the earthy, or most weathered portion of muscovite was taken, being preliminarily sifted through a 0.06 mm mesh and next finely ground in an agate mortar.

Table 1

Chemical Composition of Tchupa Muscovite

	Muscovite unchanged by weathering			Muscovite which underwent weathering		
	%	Partial ratio		%	Partial ratio	
SiO_2	43.50	0.724	2.13	44.48	0.741	2.23
Al_2O_3	34.67	0.340	1.0	33.81	0.332	1.0
Fe_2O_3	4.91	—	—	4.83	—	—
CaO	0.16	—	—	0.50	—	—
MgO	0.64	—	—	0.93	—	—
$K_2O(Na_2O)$	9.83	—	—	8.75	—	—
H_2O constit.	6.14	0.341	—	6.36	0.353	—
	99.85	—	—	99.66	—	—
H_2O hygroscop.	2.22	—	—	2.10	—	—

Upon treatment of the finely ground part by the 5% soda solution with heating in a water bath during 1 hour, the solution was found to contain: SiO_2—0.250%, Al_2O_3—0.479%.

After treatment with soda, the material was treated with a 10% HCl solution followed by heating in a boiling water bath during 10 hours; upon filtration and washing the residue was treated with a 5% soda solution, this being done with a view to extract the SiO_2 resulting from the disintegration of the weathered muscovite. The chemical composition of the disintegrated portion was found to be as follows (Table 2, in %):

Table 2

		Partial ratios	
SiO_2	17.08	0.282	4.5
Al_2O_3	6.56	0.064	1.0
Fe_2O_3	9.11		
CaO	0.62		
MgO	0.96		
$K_2O(Na_2O)$	4.46		
H_2O constit.	6.32		
H_2O hygroscop.	2.82		
	47.95		
Unchanged residue	53.00		
	100.95		

Table 3

		Partial ratios	
SiO_2	24.88	0.414	1.84
$Al_2O_3(Fe_2O_3)$	22.79	0.255	1.0
CaO	0.18		
MgO	0.14		
R_2O accord. to res.	8.38		
H_2O constit.	5.89		
H_2O hygroscop.	1.11		
Unchanged residue	36.69		

Treatment of the Non-Weathered Tchupa Muscovite with 10% HCl. After treatment of the non-weathered muscovite with muriatic acid and subsequent leaching out of the liberated SiO_2 with soda, a residue amounting to 36.606% was obtained. In the disintegrated part there was found (Table 3, in %).

Besides the above-mentioned, an incomplete analysis of the most decomposed part of the muscovite with an earthy appearance was also accomplished. This portion was obtained by means of sifting the disintegrated muscovite flakes through a 0.06 mm mesh. It contained (Table 4, in %):

CaO, MgO and R_2O were not determined. Judging by the sum of the oxides found in result of the analysis, about 4.80% falls to the share of the above oxides. If the amounts of CaO and MgO found with other analyses (1—1.5%) are taken into consideration, only a little more than 3% will be found to fall to the share of alkalies.

Table 4

SiO_2	62.85
TiO_2	0.66
Al_2O_3	13.76
Fe_2O_3	5.46
H_2O (loss upon ignition)	12.48
Total	95.20
H_2O hygroscop.	2.72

Muscovite Obtained from the Church Ruins in the Environs of Viatka. The laminae of this muscovite are in their outward appearance indistinguishable from those of Tchupa. They are just as colourless and transparent, similarly flexible in their middle portions, while on the periphery they are coloured brownish-yellow by iron hydroxide, and they are also brittle. In view of such a similarity with the Tchupa muscovite, the Viatka muscovite was subjected to a less detailed chemical investigation. The chemical composition of only that part of the muscovite was determined which had been decomposed under treatment with 10% HCl. Constitutional and hygroscopic water was also determined.

Treatment of the Weathered Part of the Viatka Muscovite with 10% HCl, with heating in a water bath during 10 hours. Composition of the disintegrated part of the muscovite (in terms of air-dry sample) (Table 5, in %):

Table 5

SiO_2	15.47
Al_2O_3	5.16
Fe_2O_3	7.00
CaO	0.51
MgO	0.51
R_2O	6.29
H_2O constit.	7.13
H_2O hygroscop.	0.98
	42.08
Res. from treatment with soda and HCl	56.86
Total	99.94

Partial ratios

0.257 4.64
0.051 1.0

Comparing the total composition of the muscovite exposed to weathering with the non-weathered muscovite, we see that though there exists but a comparatively small difference between them, yet this difference is very markedly expressed. Primarily, the total content of SiO_2 in weathered muscovite is higher than in non-weathered muscovite (44.48 and 43.50%, respectively). On the other hand, the amount of Al_2O_3 in non-weathered muscovite exceeds that in weathered muscovite (34.67 and 33.81%, respectively). The same holds true also for alkalies (in weathered muscovite the respective figure is 8.75%, while in non-weathered muscovite it reaches 9.83%). As regards other oxides, we notice, on the contrary, an increase in the amount of H_2O, CaO and MgO in weathered muscovite. The increase in the contents of H_2O and MgO is here altogether normal, since a similar phenomenon is observable in many cases in the weathering of silicates. The increase of the amount of CaO in muscovite subjected to weathering should be considered normal, since Ca (as well as Na) is most easily subjected to leaching in silicates. In this case Ca may possibly have an adsorptive character.

Thus, total chemical analysis shows that the weathering of muscovite under the conditions of moderately cold and humid climate leads to the leaching out of predominant quantities of Al_2O_2 and alkalies and to the accumulation of SiO_2, MgO and H_2O in the residual product.

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MINERALOGY

FLUORITE IN THE KUNGUR DEPOSITS OF TATARIA

By L. M. MIROPOLSKY

(Communicated by A. E. Fersman, Member of the Academy, 5. X. 1939)

Within the last years segregations of fluorite in the Permian deposits of the Soviet Union were discovered in a number of places. They were described as early as in 1928 by Prof. Krotov (3) who found them in Upper Permian deposits near the village Repanovsky on the Northern Dvina River (according to the materials of Prof. B. K. Likharev). Somewhat later a description was provided by Uspensky (4) of fluorite occurring in Lower Permian deposits near the village Kabanie-Karino on the Eastern slopes of the Urals. Prof. Baturin (1) also found such segregations of fluorite in the district of the «Zamiatino» dome on the Emba River, 180 km north of Akmolinsk. Segregations of fluorite in Permian deposits of Western Europe had been known even much earlier, for instance, in the red layers of Hemnitz, in the middle zechstein near Römmerstein (the Southern Hartz, near Zachs), in the upper zechstein of Elmshorn near Liège. The same must be said also of several localities of Central Africa and Northern America.

The mentioned deposits of fluorite in the Permian formations of the Soviet Union are representative in that particular respect that all of them are associated with halogenous formation, such as gypsum, celestine and their congeners. Taking into account both this joint occurrence and the availability of large halogenous formations with the same mineral complex in the Permian deposits of Tataria, it would seem more than plausible to assume the existence of fluorite here, too. However, a careful survey of all the exhibits available at the geological and mineralogical museum of the Kazan University carried out a few years ago failed to give any results in this direction, and it was only in the beginning of 1939, in course of studying the halogenous formations from bore-hole No. 6 located on the right bank of the Kama near the landing stage of the village Sokoliy Gory, that the writer succeeded in finding fluorite deposits. These were discovered in the lower part of Kungur formations among dolomites in two cores: No. 89 taken from a depth of 120.42—121.02 m, and No. 92 taken from a depth of 126.64—130.57 m, at an absolute mark of the bore-hole head—54.27. In both cases the dolomite represents macroscopically a fine-grained dense, sometimes slightly porous rock, grey in colour and filled with gypsum concretions. Under the microscope the dolomite from both cores appears as a fine-grained mass, the form of the separate grains of which is for the most part anhedral and more seldom euhedral, in the shape of regularly bounded rhombohedra. The size of both kinds varies from 0.01 to 0.03 mm. The groundmass of the section discloses: a) rather frequent gypsum concretions, b) occasional chalcedony (lutecite) and quartz concretions in the form of regular spherolites.

The first layer of the fluorite-bearing dolomite is overlain by anhydrite, occasionally metamorphozed into gypsum, with a thickness of 3.92 m, and it is again underlain by gypsum of a thickness of 2.70 m with relict anhydrite inclusions. On top of the second layer of the fluorite-bearing dolomite a stratum of gypsum is to be found containing anhydrite relicts of a thi-

ckness of 2.02 m, while below it dolomite with big gypsum concretions occurs. The chemical composition of fluorite-containing dolomite see in the table.

In both layers of dolomite fluorite forms inclusions in gypsum, where, along with it, separate scattered rhombohedra of dolomites, as well

Depth of sampling	Chemical and mineralogical composition										
	H_2O up to 60°C	Loss on ignition up to 250°C	Insoluble residue	R_2O_3	CaO	MgO	SO_3	$CaSO_4 \cdot H_2O$	$CaSO_4$	$CaCO_3$	$MgCO_3$
120.42—121.02 m . .	0.17	5.47	0.83	0.07	31.46	15.41	14.34	26.14	3.72	38.31	32.23
126.64—130.57 m . . .	0.25	2.16	0.76	traces	30.90	18.91	7.66	10.32	4.86	45.88	39.55

as relict stray pieces of anhydrite and anhedral grains of celestine are to be found. In gypsum concretions fluorite inclusions appear, first, as separate scattered crystals having the form of cubes, sometimes regularly built and sometimes slightly elongated in one or other direction; and secondly, as small aggregate gatherings accumulated into groups. In the latter case the fluorite crystals can also be clearly seen to be crystallized as cubes. The size of the separate crystals of fluorite varies from 0.03 to 0.1 mm. In passing light these crystals generally appear colourless and only sometimes show a slightly discernible pink hue. Octahedral cleavage is clearly visible on almost all crystals, taking the form of mutually perpendicular intersecting lines. With crossed Nicol prisms fluorite is isotropic and in this case its crystals stand out sharply against the gypsum background, taking the form of black squares and rectangles. The index of refraction of fluorite when determined in immersion liquids is equal to 1.432. The non-soluble residue, obtained upon heating fluorite in a platinum crucible with strong sulphuric acid, gives out vapours of hydrofluoric acid which etch the glass covering. The chemical composition could not be determined for lack of material.

The above-mentioned geological conditions of the occurrence of fluorite-bearing dolomites among halogenous formations, as well as the fact that fluorite inclusions were found in gypsum associated with anhydrite and celestine, give ample grounds to stand to the syngenetic origin of both fluorite and rocks surrounding this mineral, its provenance being connected with chemogenous precipitation of concentrated brines in the Kungur Sea which had once been located there. This point of view explaining the genesis of fluorite was formerly expounded in a most convincing manner by W. Mackie for relict Triassic basins, while the same views were advocated later by Krotov, Uspensky and Baturin for the Permian deposits of the Soviet Union. However, taking into exact account, on the one hand, the mutual relations of gypsum, fluorite and the rocks usually accompanying them, and on the other hand, the mutual relations of these rocks to dolomite, it would appear that the crystallization of fluorite coincided more closely with the moment of the crystallization of dolomite and celestine, since gypsum—and formerly anhydrite—had the function of cementing, as it were, all these formations into a somewhat more advanced phase.

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MINERALOGY

GOYAZITE IN THE BRECCIA OF THE ROMNY AND ISSACHKI SALT DOMES

By Z. N. PITKOVSKAYA

(Communicated by W. I. Vernadsky, Member of the Academy, 3. X. 1939)

In the course of a petrographic study of the rocks from a breccia of the Ukrainian salt domes (Romny, Issachki) the presence of a rare mineral, goyazite, has been established in a heavy mineral concentrate after a separation wiht Thoulet solution, specific gravity 2.9.

The mineral is of a trigonal system with a characteristic habit in the shape of well developed clearly zonal rhombohedra. The grain size varies from 0.05 to 0.25 mm on the average. The refractive index of the mineral along *Ng* varies from 1.640 to 1.642 and along *Np* from 1.634 to 1.636. In convergent light there may be easily seen a clear-cut cross of a positive character. Colourless. In thick grains slight pleochroism *X*—light pink, *Z*—light yellow and greenish is frequently observed. Individual zones of the mineral are distinguished by the refractive index and colouring, being sometimes colourless and sometimes slightly pleochroic. The birefringence value as calculated from the refractive index difference is about 0.007—0.008.

On the basis of the above highly characteristic optical features the mineral has been identified as goyazite referring to the alumophosphate group with the following chemical formula:

$$2SrO \cdot 3Al_2O_3 \cdot 2P_2O_5 \cdot 7H_2O.$$

The optical determination of goyazite has been confirmed by microreactions and chemical analysis which showed the presence of phosphorus and strontium in the mineral.

The amount of goyazite in the breccia is not very large on the whole: from individual grains to 10% heavy concentrate. Less frequently this mineral predominates.

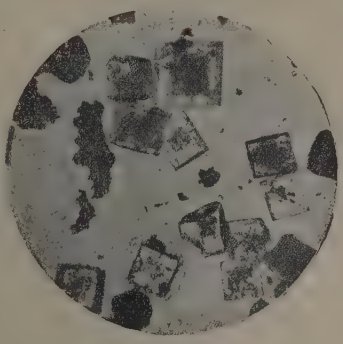
Goyazite has been encountered chiefly in an ancient Paleozoic breccia in association with authigene barite, pyrite, quartz, sometimes tourmaline. Separate goyazite grains have been observed also in some rocks of the Paleogene and Quaternary age. Evidently, the presence of this mineral in younger rocks is due to the erosion of the ancient breccia during the Tertiary and Quaternary time.

A petrographic study makes it possible to establish the presence of widely developed atmospheric erosion processes (1) in the breccia. In some areas near the contact with diabases breaking through the breccia these processes are overlapped by higher temperature phenomena connected with the intrusion (Morozevich, Korovnichenko).

As secondary minerals formed as a result of surface alterations in the breccia, the following were found: calcite, dolomite, magnesite, gypsum, halite and minerals of the silica group. These are represented by low-temperature varieties: opal, fibrous lutecite (?) and α-quartz with very irregular, non-uniformly developed faces of the prism and two rhombohedra.

In cases of more considerable accumulations of goyazite (the latter predominating over all other minerals in the heavy concentrate), there is observed a presence of a peculiar variety of a high-temperature quartz characterized by a regular pyramidally elongated shape of the crystals, terminating at both ends with rhombohedra. This quartz is clearly distinguishable from the low-temperature quartz distributed in other areas of the breccia.

The formation of goyazite as a secondary mineral is confirmed by the presence in it of a considerable amount of pyrite and clayey substance inclusions, trapped evidently during the period of crystallization from the surrounding sedimentary rocks.



Goyazite with pyrite, ×80.

Most probable seems nevertheless the formation of goyazite at high temperatures connected with the penetration of a diabase intrusion. At the same time a supply from igneous rocks must not necessarily take place, since in the breccia-like argillaceous carbonate beds saturated with salts there was sufficient material for the formation of this mineral. In particular, the presence of celestine in the breccia suggests the presence of strontium which may be transferred under conditions of atmospheric erosion; in more complex environments this might have led to the formation of goyazite which is composed, beside strontium, of phosphorus and aluminium.

The association of goyazite with silica, pyrite and sometimes tourmaline, as well as the sequence of formation of these minerals, are at present still insufficiently clear, since these minerals are encountered in very small quantities, detected only in recovering heavy concentrates, while they still failed to be detected in thin-section.

It is of interest that goyazite is a very rare mineral and has been encountered in considerable quantities only in diamond placers of the Congo ([2]) and Brazil ([3]), where its presence has been first established.

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PETROGRAPHY

MEAN CHEMICAL COMPOSITION OF THE GRANITOIDS OF THE ZERAVSHAN-GUISSAR MOUNTAIN RANGE (MIDDLE ASIA)

By I. V. BELOV

(Communicated by A. E. Fersman, Member of the Academy, 15. X. 1939)

The present paper contains the results of the treatment of chemical analyses published in the literature and also of the analyses performed by the author (1), dealing most with Kara-Tyube.

In the structure of the Zeravshan-Guissar mountain range a prominent part is taken by acid intrusions with which a number of beds of minerals are genetically associated. The petrology and the petrochemistry of these intrusions have as yet been but scantily investigated (1,2,5,7,8,10,11). The generalizations made with the help of the available materials lead to the conclusion that the Variscian inclusions of Zeravshan-Guissar mountain range will, both in respect of separate regions and when viewed as a whole, be characterized by a great peculiarity of chemical and mineralogical composition, and also by specific structural conditions which make them stand out distinctly among the intrusive formations of other ages. Certain lawful regularities in the changes in the composition of Variscian intrusives with time can also be observed, which will possibly permit in the subsequent to distinguish intrusions of different age from a petrochemical point of view.

The mean chemical composition of the granitoids of this region reflects clearly the main peculiarities of their mineralogical composition; the latter become still more clearly manifested if the mean chemical data for them are compared to the mean composition of world pre-Cambrian granite, the pre-Cambrian granite of Sweden, the granite of all periods, post-Cambrian granite, calcareous-alkaline granite, granite and orthogneiss of the Ural geosyncline and the hybrid granite-gabbro of the Shiguir-Taratash range on the western slope of the Middle Urals (Tables 1 and 2).

For comparing the mean analyses given in Tables 1 and 2 we produce below the mathematical factors and projection indices calculated according to the systems of A. N. Zavaritsky (4) and P. Niggli (13) (Tables 3 and 4).

Analyses used: 1) The mean chemical composition of granites from Nura-Tau (5 analyses) (6). 2) The mean chemical composition of granites from Kara-Tyube (9 analyses) (1, 7, 11). 3) The mean chemical composition of small intrusions of the Zeravshan chain (7 analyses) (1, 2). 4) The mean chemical composition of the granite intrusions of the Guissar chain (15 analyses) (8, 10). 5) The mean chemical composition of the granitoids of the Zeravshan-Guissar mountain system; the above-mentioned 36 analyses. 6) The mean chemical composition of the hybrid granite-gabbro from the Shiguir-Taratash range on the western slope ot the Middle Urals (9). 7) The mean chemical composition of granites and orthogneisses of the Ural geosyncline (8 analyses) (12). 8) Calcareous alkaline granite, mean composition from 20 analyses after Daily (3). 9) Post-Cambrian granite, mean composition from 184 analyses after Daily (3). 10) Granite of all periods, mean composition from 546 analyses after Daily (3). 11) Pre-Cambrian granite of Sweden, mean composition from 114 analyses after Daily (3). 12) World pre-Cambrian granite, mean composition from 47 analyses after Daily (3).

Table 1

Mean Chemical Composition of the Granitoids of the Zeravshan-Guissar Mountain System

Oxides	Analyses				
	1	2	3	4	5
SiO_2	68.87	69.07	61.55	63.76	66.06
TiO_2	0.86	—	0.55	0.36	0.55
Al_2O_3	15.46	14.76	14.74	15.55	15.13
Fe_2O_3	2.37	2.62	4.23	1.27	2.62
FeO	1.69	2.24	3.36	1.84	2.30
MnO	—	—	0.10	0.12	0.11
MgO	1.58	0.95	2.84	1.27	1.66
CaO	3.51	2.03	4.59	2.74	3.20
Na_2O	3.34	6.65	2.66	3.40	4.01
K_2O	3.15	3.10	3.28	4.14	3.47
Total	100.53	101.45	95.90	94.45	99.11

Table 2

Closest Types of Granites

Oxides	Analyses						
	6	7	8	9	10	11	12
SiO_2	66.23	71.12	69.82	70.28	70.77	70.33	71.56
TiO_2	0.64	0.02	0.41	0.34	0.39	0.54	0.48
Al_2O_3	15.02	14.01	14.53	15.10	14.59	13.86	14.20
Fe_2O_3	1.65	1.58	2.00	1.63	1.58	2.19	1.47
FeO	3.52	1.49	1.68	1.67	1.79	1.89	1.65
MnO	0.08	0.02	0.12	0.11	0.12	0.26	0.18
MgO	2.41	0.99	1.16	1.09	0.89	0.85	0.59
CaO	3.12	2.09	2.21	2.22	2.01	2.22	1.98
Na_2O	3.46	3.99	3.51	3.31	3.52	3.19	3.26
K_2O	3.78	3.87	4.26	3.98	4.15	4.41	4.53
Total	99.91	99.18	99.70	99.70	99.71	99.74	99.90

Table 3

Mathematical Coefficients after A. N. Zavaritsky

Analyses	Coefficients					
	a	*c*	*b*	*s*	*n*	*Q*
1	11.2	4.3	6.1	78.2	6.2	+29.9
2	18.3	0.4	7.6	75.6	7.6	+12.3
3	10.7	4.5	12.8	72.6	5.4	+18.7
4	14.1	3.4	5.3	77.1	5.5	+22.7
5	12.9	3.0	9.3	74.1	6.3	+20.1
6	12.7	3.4	9.1	75.0	5.8	+21.0
7	14.0	2.0	4.9	78.9	6.1	+26.0
8	13.2	2.6	5.3	77.0	6.5	+26.9
9	12.4	2.5	5.7	78.8	5.6	+30.9
10	13.1	2.3	5.2	78.5	5.6	+29.4
11	13.0	2.3	5.4	79.1	5.2	+20.1
12	13.3	2.3	3.2	80.4	5.2	+32.7

Table 4

Projection Indices after P. Niggli

Analyses	*Si*	*Al*	*fm*	*C*	*Alk*	*K*	*Mg*	*C/fm*
1	302	40.0	24.0	16.0	21.7	0.38	0.54	0.66
2	273	35.7	20.6	9.1	34.4	0.23	0.43	0.44
3	213	30.0	35.0	17.0	18.1	0.45	0.58	0.48
4	284	41.0	20.0	12.8	27.0	0.44	0.55	0.64
5	250	33.6	30.0	13.0	23.1	0.36	0.60	0.43
6	255	34.1	30.0	13.0	22.3	0.41	0.54	0.43
7	337	39.0	20.0	10.8	30.2	0.38	0.50	0.54
8	327	40.0	22.2	10.7	30.0	0.45	0.55	0.48
9	331	41.9	20.4	11.0	26.6	0.43	0.52	0.54
10	332	40.4	20.8	10.2	28.5	0.44	0.47	0.49
11	329	38.0	22.4	11.0	22.1	0.47	0.43	0.49
12	355	41.4	17.1	10.8	30.3	0.47	0.30	0.63

The separately calculated monovalent elements designated by the symbol R', bivalent elements R'' and tervalent elements R''' are recalculated to 20*. This conversion is given in Table 5.

Table 5

Valency Groups of Above-Mentioned Chemical Analyses of Granitoids

Analyses	Coefficients			Molecular number of quadrivalents
	R'	R''	R'''	
1	4.5	6.6	8.9	1 195
2	7.4	4.7	8.2	1 150
3	3.5	9.0	7.5	1 055
4	5.4	6.0	8.6	1 182
5	4.8	7.6	7.6	1 130
6	4.6	8.0	7.4	1 137
7	6.0	5.8	8.2	1 191
8	6.0	5.3	8.7	1 185
9	5.4	5.3	9.3	1 188
10	5.6	5.0	9.4	1 202
11	5.7	5.2	9.1	1 192
12	6.2	4.3	9.5	1 219

The material given above testifies to the Zeravshan-Guissar granitoids representing from a chemical point of view peculiar intrusive rocks characterized by the following principal features:

1. A rather low content of silica relatively to the mean for world type granites and a fluctuation of indices after Niggli from 213 to 302 with a mean content of silicon in the whole system equalling 250. These data correspond closely to the characteristic of the Variscian hybrid Shiguir-Taratash range on the western slope of the Middle Urals; the latter presents peculiar interest in that its Variscian age is rather convincingly determined (9). The mean acidity coefficient after Zavaritsky equals +20.1, the acidity coefficient of the above stated Shiguir-Taratash range equalling +21.0.

2. A somewhat increased content of calcium, this element playing a comparatively small part in the group of bivalent elements. The mean coefficient C of the Zeravshan-Guissar mountain range is equal to 13.0, while world type granites show fluctuations of the same coefficient from 10.2 to 11.0.

3. A relatively smaller content of alkalies (*Alk* somewhat less than half *Al*). In the world types *Alk* is by far less. The mean coefficient for the Zaravshan-Guissar mountain system equals 0.36, while for world type granites the respective value fluctuates from 0.38 to 0.47. Hence the granitoids under consideration are reacher in Na than the world types. Coefficients R', R'' and R''' afford the possibility to ascertain that with respect to the group of other oxides the content of alkalies in these granitoids is somewhat enhanced, viz. the ratio $R' : (R'' + R'')$ is about as 1 : 3.0.

* The method of calculation applied consists in molecular quantities R' (Na_2O+K_2O), R'' ($FeO+MnO+CaO+MgO$) and R''' ($Al_2O_3+Fe_2O_3$), being summed up into groups and recalculated to 20 after the formula: $\frac{R^{n}\,20}{\Sigma}$.

4. A relatively high content of iron and in general a relative enhancement of the *fm* group, since the mean *fm* coefficient for the granitoids of the system under consideration equals 30.0. The fluctuation of the *fm* coefficient in world type granites is from 17.1 to 23.4.

According to A. N. Zavaritsky, such conditions find their reflection in a characteristic increase of coefficient *b*, which equals 9.3. The mean coefficient *b* for world type according to Daily([3]) comes to 3.2—5.7 and, accordingly, for the rocks investigated the increase of coefficient *b* falls already out of the scope of the usual fluctuations.

In connexion with the enhanced content of iron, a pronounced tendency towards increased content of titanium is observed in the granitoids of the Zeravshan-Guissar mountain system—a fact which is in full conformity with the geometrical affinity of this element to iron.

5. A lowered content of monovalent elements (the mean for the R' system is equal to 4.8), this being at the expense of potassium; it is only the granites of Kara-Tyube that have an enhanced content of monovalent elements, with R' equal to 1, which is connected with the hybridization of the granitoids of the given system at the expense of their assimilating argillaceous rocks. In respect of monovalent elements these granites can be compared with the hybrid granite-gabbro Shiguir-Taratash range.

6. An enhanced content of bivalent elements throughout the mountain system for which R'' is equal 7.6. It is of interest to note that the pre-Cambrian world granite is characterized by R'' equal to 4.3, while post-Cambrian granite has the same figure at 5.3.

The above-mentioned data permit of making the tentative conclusion that intrusions differing in respect of their age in mean figures possess a different content of bivalent elements, too, pre-Cambrian intrusions holding a smaller number of these than Paleozoic intrusions.

It is obvious that in respect of the R'' coefficients, the granitoids of the Zeravshan-Guissar mountain range stand closer to Ural (Paleozoic) hybrid intrusions.

From a mineralogical point of view, the above-mentioned chemical peculiarities of the granitoids of the Zeravshan-Guissar mountain system can be viewed as the predominance in them of rocks rich in potassium feldspar, which mineral stands out everywhere sometimes occurring even with a plagioclase edge. It is most characteristic that along the potassium feldspar, hornblende also makes its appearance.

All these peculiarities bring out forcibly certain general features of the chemical composition of Variscian acid intrusions which are clearly manifest in the mean chemical composition of these formations. Hence it would seem that the conclusions ventured above are apt to acquire a definite petrographic and, possibly, even a correlative importance.

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PETROGRAPHY

ALKALINE ROCKS OF THE OZERNAYA VARAKA OF THE KHABOZERO REGION (SOUTH-WESTERN PART OF THE KOLA PENINSULA)

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The alkaline rocks in the region of the Khabozero station of the Kirovsk railway were first discovered by the author in 1935. A small massif with an area of 1 km² occurs amidst Archaean orthogneisses on the Ozernaya Varaka 2 km south-westward of the Khabozero station. The schistosity of the orthogneisses strikes in a latitudinal direction with angles of dip of 30—45° to the north. The intrusions into the crystalline basement of the Archaean were preceded by strong tectonic movements in the post-Caledonian epoch of folding.

In addition to the Ozernaya Varaka, two large massifs of ultrabasic and alkaline rocks are known in the region, with a total area of 30 km². One of these is a massif of olivinites on the Lesnaya Varaka near the Khabozero station with melanite-nepheline rocks at the contact with perovskite olivinites; the other is an intrusion of pyroxenites near the Africanda station, with economic deposits of perovskite, with nepheline rocks having much in common with the rocks of the named massifs of the Khabozero region.

Within 1 km² of the alkaline massif of the Ozernaya Varaka a great variety of petrographic types is observed. In the massif three groups of rocks are sharply distinguished.

1. Rocks of the central part of the massif, in which the melanocratic component quantitatively predominates over all the other components.

2. Near-contact zone of development of nephelinic and feld-spar-cancrinitic rocks—ijolites, urtites and cancrinitic syenites.

3. Zones of contact-metamorphic rocks—with carbonate, nephelinic, melanitic, wollastonic and feldspar rocks.

Standing apart are vein bodies inside the massif, represented by carbonatite, cancrinitic syenites, nepheline, natrolite and micaceous pegmatite.

I. Rocks of the Central Part of the Massif. 1. The most wide-spread rocks in this part of the massif are the rocks of the pyroxenite group. The content of pyroxene —titan-augite—in the rock is 70—82%. The other minerals quantitatively vary within the following range: amphibole, from 1 to 10%; nepheline, for 0.5 to 14%; titaniferous magnetite, from 1.5 to 10.5%; perovskite, from 1 to 7%; apatite, from 0.5 to 13.5%. Moreover, in the rocks an insignificant percentage of biotite, calcite and sphene is always present.

2. Melteigites occur mainly in the marginal part of the pyroxenitic body in the shape of small islands as a rock transitionary to ijolites. An analogous of such a rock was described by Brögger in 1921 from the Fen

Table 1

Chemical Composition of Rocks of the Alkaline Massif of Ozernaya Varaka

Oxides	Pyroxenite	Pyroxenite with sulphides	Pegmatoid pyroxenite	Ijolite	Melanitic ijolite	Biotitic cancrinitic syenite	Pyroxenic cancrinitic syenite	Pyroxenic cancrinitic syenite	Carbonatite	Fenite
	I	II	III	IV	V	VI	VII	VIII	IX	X
SiO_2	33.58	40.24	38.06	37.53	39.64	57.03	52.31	48.56	18.61	51.82
TiO_2	6.56	2.61	3.49	3.54	2.37	0.37	0.46	0.48	0.18	traces
Al_2O_3	6.18	7.12	5.48	14.00	17.02	20.01	18.66	21.22	4.01	20.79
Fe_2O_3	9.80	6.60	9.27	7.67	6.06	1.54	1.10	3.42	1.69	0.31
FeO	6.94	6.14	7.83	5.05	4.76	2.80	2.14	1.40	0.71	1.13
MgO	8.65	9.55	9.92	6.33	3.46	0.41	1.01	1.19	0.63	0.24
CaO	21.18	21.43	18.25	15.77	13.53	1.36	4.72	5.70	38.95	6.62
MnO	0.61	0.10	0.12	0.05	0.11	0.02	0.03	0.03	0.13	0.02
K_2O	0.33	0.60	1.13	1.81	2.72	3.91	3.38	2.05	0.72	2.09
Na_2O	1.81	2.30	2.23	6.32	8.63	10.56	11.90	10.81	2.70	10.65
P_2O_5	2.19	1.61	0.14	1.05	1.22	0.07	0.05	none	0.33	0.94
V_2O_5	0.08	0.067	undet.	traces	undet.	undet.	undet.	undet.	undet.	undet.
NiO	traces	traces	»	not found	»	»	»	»	»	»
S (total)	0.32	0.87	»	0.07	»	»	»	0.15	»	»
CO_2	0.91	0.72	3.19	0.81	0.50	1.32	2.10	4.31	30.39	4.73
F	undet.	undet.	undet.	undet.	undet.	undet.	undet.	0.15	undet.	undet.
Cl	»	»	»	»	»	»	»	0.28	»	»
$HO_3^{-110°}$	0.10	0.12	0.12	0.18	0.14	0.16	0.14	—	0.11	0.10
$H_2O^{+110°}$	1.16	0.47	0.91	0.50	0.64	1.12	1.53	0.28	0.34	1.15
Total	100.31%	100.55%	100.14%	100.69%	100.85%	100.71%	99.53%	100.09%	99.51%	100.59%
Sp. gr.	3.44	3.30	3.29	3.22	3.03	2.64	2.77	—	2.74	2.60

Note. Analyses I, II, III, IV, V, VI, VII, IX and X made by a group of analysts of the Leningrad Mining Institute under the supervision of Prof. Saldau. Analysis VIII made at the laboratory of the «Apatite» Combinate, Kirovsk.

region of Norway. The Khabozero melteigite contains 47—50% titan-augite, 25—35% nepheline + cancrinite, 5% amphibole, 1% biotite, 3.5% titaniferous magnetite, 0.5% calcite, 1.5% sphene, 2.5% apatite, from 0.3 to 10% perovskite and melanite.

II. Nepheline and Feldspar-Cancrinite Rocks of the Near-Contact Zone. 1. The main rock of the near-contact zone is ijolite. It contains 39% titan-augite, 54% nepheline, 1% amphibole, 3% titaniferous magnetite, 1% apatite, 0.3% sphene and perovskite, melanite, sodalite. Here also a belt of melanite and perovskite ijolites has been found. The former contain up to 13% melanite, in the latter 10% perovskite is contained. The structure of the rock is a poikilitic one.

2. Urtites. Comparatively poorly developed in the massif and occurring only as small islands amidst ijolites.

3. Biotite and Pyroxene-Cancrinite Syenites. They occur in the form of bed veins and transecting veins among ijolites and urtites. The thickness of the bed veins does not exceed 2 m, and their length is 80—100 m. The transecting veins fill up the joints in the rocks of the massif, mainly of a north-eastern and north-western strike. Their thickness is 5—10 cm. The trachytoid nature in cancrinitic syenites of bed veins is distinctly pronounced with an orientation to the north-west and a dip to the south-west at an angle of 25°. Thus, the dip in the rocks of the massif is a reverse one to the dip of the orthogneisses, enclosing the massif. The high content of primary cancrinite in the syenites (18—22%) indicates the richness of the melt in carbonic acid.

III. Rocks of the Zone of Contact. The rocks of the contact halo are distinguished by a particular diversity. The most widespread are syenitized orthogneisses—fenites. Analogous rocks have been described by Brögger from the Fen region at the contact of alkaline massifs with orthogneisses.

1. The chief mineral of fenites—microcline-perthite together with albite makes up 70—75% of the total composition of the rocks. Aegirite-diopside and biotite constitute 25—20%. A considerable part of the remaining 5% of the rock is made up by calcite and apatite, and cancrinite and pyrrhotite are present in insignificant amounts.

2. Pyroxene-Carbonate Rocks. The chief mineral of the rock, aegirite-diopside, makes up 65—75%, calcite 34—24% of the rock; it is xenomorphous and includes idiomorphous plates of pyroxene. In an amount up to 1% apatite, zeolitized nepheline and sulphides are always present in the rock. This rock in its composition closely approaches ringite, described by Brögger in 1921.

3. Carbonate-Pyroxene Rocks. They contain 55—75% calcite, 42—22% aegirite-diopside. The accessory minerals, perthite, zeolitized nepheline, cancrinite, apatite and sulphides make up about 3% of the total.

4. Carbonatites form close veins and pockets of an insignificant thickness. They consist of 49% calcite, 40% perthite, 10% aegirite-diopside, and about 1% sphene, apatite, zeolitized nepheline and sulphides.

The above do not exhaust the list of petrographic types of the contact zone. In addition to those listed above, at the contact of the northern part of the massif carbonate-melanite rocks with aegirite-diopside have been met with and nephelinic rocks are widely developed. Frequently occur melanitic melteigites with a melanite content up to 30%, sphenic melteigites with a sphene content up to 10%. The nepheline is zeolitized. Ijolites are developed to the same degree as melteigites. The presence at the contact of the northern

part of the massif (pit No. 5) of wollastonitic ijolites should be noted. The thickness of the belt of wollastonitic ijolites reaches 15 m.

IV. Vein Bodies of the Massif. The rocks of the alkaline massif are broken by a close network of joints, a part of which of a north-eastern and north-western direction are filled with veins of cancrinitic syenites, natrolite, nepheline, carbonatite and mica pegmatite. Veins and pockets of carbonatites are very extensively developed inside the massif. The thickness of individual veins attains 1.5—2 m.

Table 2

Quantitative Mineralogical Composition of the Rocks of Ozernaya Varaka (Alkaline Massif) (in volume per cent)

Minerals	To analysis I Pyroxenite	To anal. II. Pyroxenite with sulphides	To anal. III Pegmatoid pyroxenite	To anal. IV Ijolite	To anal. V. Melanitic ijolite	To anal. VI Biotitic cancrinitic syenite	To anal. IX Carbonatite	To anal. X Fenite	To anal. VII Pyroxene cancrinitic syenite
Titan-augite	55	81.8	47.3	37.6	—	—	—	—	—
Aegirite-diopside	—	—	—	—	—	—	—	0.4	—
Aegirite-augite	—	—	—	—	26.5	—	10.2	—	10.7
Nepheline	1.5	8.4	2.8	53.3	59.0	—	—	—	—
Cancrinite	0.7	0.3	4.1	—	—	12.9	—	14.5	19.9
Green hornblende	13.6	2.0	23.7	0.6	0.1	—	—	—	—
Microcline, microperthite and perthite	—	—	—	—	—	82.2	—	73.4	68.7
Biotite	0.3	0.1	7.4	—	0.1	4.1	40.5	—	0.3
Titaniferous magnetite	10.8	—	8.6	3.3	0.1	—	—	—	—
Perovskite	11.0	0.8	0.1	3.5	—	—	—	—	—
Calcite	1.4	0.1	3.1	—	0.2	—	48.3	10.2	—
Melanite	—	—	—	—	13.4	—	—	—	—
Sphene	1.1	—	2.6	0.2	—	—	0.5	—	—
Apatite	4.6	3.3	0.3	1.5	0.6	—	0.2	1.2	0.3
Pyrrhotite	—	3.2	—	—	—	0.8	0.3	0.3	0.1

In order to explain the origin of the complex of the ultrabasic and alkaline rocks of the Khabozero-Africanda region, it should be assumed that the original magma was an ultrabasic one, enriched with alkalies of titanium, with the volatile components playing an active rôle. Within a comparatively small area of the Khabozero-Africanda region (100 km²) three intrusive bodies lie among Archaean orthogneisses almost along one line, stretched along the schistosity of the orthogneisses in a western-north-western direction. All of these bodies represent a single genetic whole, forming a complex of ultrabasic and alkaline rocks.

As the beginning of the crystallization of magma of this complex of rocks should be considered the intrusion of olivinites in the region of the Khabozero station within an area of over 20 km². In this part of the region the magma swallowed up a large mass of carbonate rocks (dolomites), a part of which has been preserved among olivinites in the shape of detached xenolyths.

Inside the massif of olivinites we meet schlieren belts of perovskite olivinites analogous to the deposit of perovskite of Africanda. In the zone of contact of the olivinite massif with orthogneisses lie fine-grained pyroxenites, analoga of which are widely developed in the pyroxenite intrusion of Africanda. Directly in the contact the aegirite-melanite rock with nepheline finds an analogon in the alkaline massif of the Ozernaya Varaka.

Having become enriched with lime, the magma acquired a still greater mobility and a capacity to differentiate. The heavy components of the magma in the shape of a silicate of magnesium and iron were the first to crystallize, with the formation of olivine always containing: CaO—0.6%, Mn—0.33%, Ti, Cr, Ni and 0.35% alkalies.

In the first stage of crystallization a considerable portion of titaniferous magnetite precipitated, with the formation of ore olivinites. The further desilification of the magma proceeded by the way of formation of lime-bearing silicates—augite, aegirite-diopside, aegirite-augite in the massifs of Africanda and Ozernaya Varaka and wollastonite in the massif of Ozernaya Varaka.

The ability of CaO, introduced into the magma, to cause an early precipitation of lime-bearing crystals, to combine silica, leads to an accumulation of alkalies in the residual melt.

Thus, a lack of SiO_2 in the residual melt caused the formation chiefly of feldspathoids, and of comparatively little K—Na feldspar in cancrinitic syenites. The alkaline intrusion of Ozernaya Varaka representing a residual melt of ultrabasic magma, saturated with alkalies and CO_2, produced a varied series of feldspathoid and feldspar-cancrinitic rocks—melteigites, ijolites, urtites and cancrinitic syenites.

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PETROGRAPHY

OLIVINITES OF THE KHABOZERO REGION (SOUTH-EASTERN PART OF THE KOLA PENINSULA)

By V. A. AFANASSIEV

(Communicated by A. E. Fersman, Member of the Academy, 5. X. 1939)

The intrusion of the Khabozero olivinites on the Lesnaya Varaka is situated 4 km south of the Khabozero station of the Kirov railway on the south-western shore of Lake Saigozero, rising 120—140 m above the country which presents a swamped plain. This varaka, and together with it the intrusive body, are stretched in a north-western direction, comformably to the strike of schistosity of the enclosing massifs of the Archaean and oligoclase orthogneisses which have a strike of schistosity 280° NW, dipping NE at an angle of 40—45°.

The area of the whole intrusive body is about 20 km²; of these 12 km² fall to the share of olivine rocks, the remainder being composed of pyroxenites, pyroxene-feldspar rocks and pyroxene-melanite rocks of the zone of contact.

The structure of the ultrabasic intrusion is a zonal one. The central zone, on the most elevated portion of the Lesnaya Varaka, is composed of olivine rocks, among which the following may be distinguished: titaniferous-magnetitic, perovskitic, oreless fine-grained and pegmatoid olivinites and olivinic-titaniferous magnetites. The intermediate zone, between Archaean acid rocks and olivinites, is represented by normal pyroxenitic and pyroxene-feldspar rocks with a variable thickness from 80 to 250 m.

Finally, along the line of the contact passes a zone, 10—12 m wide, of compact fine-grained rocks containing grass-green pyroxene, melanite (35—47%), feldspars, nepheline, apatite, and pyrrhotite.

The contact of the ultrabasic intrusion with orthogneisses is sharply pronounced, with a dip to the north-east at an angle of 45°. The Archaean orthogneisses in a belt 10—15 m wide, along the line of contact have been transformed to syenites, consisting of 75—80% perthite, 15—10% pyroxene and accessory minerals: biotite, sphene, apatite, albite.

The rocks of the central zone may be subdivided into two large groups. The first group—ore olivinites, fine-grained and medium-grained, with a sideronitic structure, occupy two thirds of the area to the north-west. The second group—oreless fine-grained and pegmatoid olivinites are concentrated in the south-eastern end of the massif within an area of 3—4 km². The bulk of the ore olivinites is composed of titaniferous-magnetitic olivinites with a content of titaniferous magnetite from 5 to 60%; of olivines from 90 to 40% and of accessory minerals: perovskite, leucoxene, monoclinic pyroxene. The perovskitic olivinites and olivinic-titaniferous magnetites play a subordinate part. Their quantitative composition is given in Table 1.

Table 1

Quantitative Mineralogical Composition of the Rocks of the Lesnaya Varaka (in volume %)

Minerals	To analysis I Pegmatoid olivinite	To anal. II. Medium-grained olivinite	To anal. VIII. Titan. magnet. olivinite	To anal. IX. Olivinic-titan. magnetite	To anal. X. Perovskitic olivinite	Melanite-pyroxene rock
Olivine	98.7	95.2	43.1	18.8	56.3	—
Titan. magnetite	1.3	3.3	56.3	81.1	25.1	—
Perovskite	—	—	0.6	0.1	18.6	—
Diopside-augite	—	1.5	—	—	—	39.1
Melanite	—	—	—	—	—	47.2
Nepheline	—	—	—	—	—	7.4
Apatite	—	—	—	—	—	0.8
Pyrrhotite	—	—	—	—	—	5.5
	100%	100%	100%	100%	100%	100%

The ore part of olivinites of the central zone shows an excellently pronounced primary lamination of rocks in alternation of bands of a different composition. Thin bands of titaniferous magnetite alternate with thin bands of titaniferous-magnetitic and perovskitic olivinites. The strike of the bands is subordinate to the general direction of the intrusion to the NW with steep angles of dip from 65 to 80° to the NE.

Thus, in the ore olivinites an orientation of the components of the rocks (banding) is very frequently observed, while the oreless fine-grained and pegmatoid olivinites show a massive habit and an authallotriomorphic structure.

The oreless olivinites contain 95—98% olivine, 4.5—1.5% ore mineral, and rarely monoclinic pyroxene. The ore mineral of the pegmatoid olivinites is sharply different from the titaniferous magnetite of the ore olivinites. The titaniferous magnetite of the ore olivinites fills interspaces between the olivine crystals, while in pegmatoid olivinites the ore mineral is idiomorphic and is impregnated in olivine crystals. The titaniferous magnetite of the ore olivinites contains scarcely any Cr_2O_3, while in the ore mineral of pegmatoid olivinites Cr_2O_3 is contained in an amount of 12.49% (see analysis III in Table 2). The chief mineral of the rocks of the central zone, olivine, represents forsterite with a content of 10% of a fayalite molecule. Its constants are: $2V = +88 + 89°$; $Ng = 1.694$, $Np = 1.659$. In the ore olivinites its crystals have a rounded shape with fused faces. The cleavage is distinctly pronounced and partly in two directions.

Into the composition of pyroxene of the intermediate zone enter pyroxene, diopside of the augite series (75—85%) and titaniferous magnetite (26—15%). The structure of the rock is a sideronitic one. The angle of optical axes of pyroxene is $+54°$ with $Ng = 47°$.

Vein Bodies in the Massif of Olivinites. The olivinites are broken by numerous joints, following mainly three directions—north-western, north-eastern and latitudinal one. A considerable part of these joints are filled up by hydrothermal veins of a monomineral white rock. Its hardness is somewhat above 2; it has a greesy feel, but upon drying in open air it loses the absorbed moisture and becomes hard.

Table 2

Chemical Composition of Rocks of the Massif of Olivinites of Lesnaya Varaka of the Khabozero Region

Oxides	Pegmatoid olivinite	Pegmatoid olivinite of the oreless fraction	Ore fraction of the pegmatoid olivinite	Pegmatoid olivinite	Fine-grained oreless olivinite	Medium-grained oreless olivinite	Titan.-magnet. olivinite	Titan.-magnet. olivinite	Olivinic-titan. magnetite	Perovskitic olivinite	Kolskite
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
SiO_2	39.09	40.37	3.20	40.77	38.32	38.63	28.06	24.39	4.94	12.86	40.32
TiO_2	0.46	0.12	6.23	0.07	0.47	0.33	4.03	4.93	10.80	23.96	—
Al_2O_3	0.19	0.36	6.08	0.10	0.00	0.45	0.00	0.81	3.61	3.57	0.76
Fe_2O_3	2.23	2.10	29.55	0.85	3.32	0.74	15.07	20.65	44.63	14.09	1.82
FeO	13.10	11.62	39.08	9.81	12.98	13.87	17.23	17.06	22.65	12.92	—
MnO	0.34	0.33	—	0.26	0.22	0.08	0.11	undisc.	undisc.	0.24	—
MgO	42.90	43.55	—	47.33	42.38	41.65	33 63	31.03	12.34	16.52	36.27
CaO	0.81	0.61	—	0.42	0.88	1.35	0.65	0.13	0.10	14.53	2.44
K_2O	—	—	—	0.00	0.15	0.11	0.23	0.08	—	—	—
Na_2O	0.38	0.35	—	0.00	0.08	2.11	0.08	0.23	—	0.73	—
P_2O_5	0.15	0.00	—	0.01	0.00	0.09	0.00	traces	—	0.00	—
CO_2	0.00	0.00	—	—	—	0.10	—	0.08	0.16	—	3.35
NiO	0.05	0.04	0.21	0.18	0.24	0.17	0.13	0.34	0.27	0.00	—
Cr_2O_3	0.64	traces	12.49	—	0.07	0.09	0.07	0.47	0.01	0.01	—
V_2O_5	traces	0.00	traces	—	traces	undisc.	0.01	undisc.	traces	—	—
TR_2O_3	—	—	—	—	—	—	—	—	—	0.28	—
F	—	—	—	0.00	0.00	—	0.00	—	—	—	—
Cl	—	—	pres.qual.	0.01	0.02	—	0.01	—	—	—	—
S	qual.disc.	—	qual.disc.	—	0.03	0.04	0.04	0.05	—	0.23	15.39
$H_2O^{-110°}$	0.06	0.06	—	0.30	0.23	0.16	0.13	0.09	0.17	0.06	—
$H_2O^{+110°}$	—	—	—	0.56	0.94	0.43	0.78	0.27	0.80	—	—
Total	100.40	99.51	96.84	100.67	100.33	100.40	100.26	100.65	100.48	100.00	100.35
Sp. gr.	—	—	—	—	—	3.46	—	3.81	4.37	—	—

The specific gravity of the rock is 2.4. Its chemical composition is given in Table 2, analysis XI. This rock was subjected to an all-sided study by N. E. Efremov (1), who established that it consisted entirely of a previously unknown mineral of the serpentine group, whose place in the series of serpentine minerals is between deweylite and carachaite.

The new mineral received the name of kolskite with a chemical composition: $5MgO_2 . 4SiO_2 . 4H_2O$.

In addition to veins of kolskite, rarely veins of tremolite-humitic rock are encountered within the area of development of carbonate rocks.

Among olivinites in the north-eastern part of the massif and in the south-western contact of olivinites with orthogneisses, over an area of 500×700 m, lie amphibolites with actinolitic hornblende, olivinites entirely serpentinized and replaced by kolskite, and in the areas of development of amphibolites, xenolyths of crystalline dolomites have been preserved.

It may be assumed that the formation on the Lesnaya Varaka of amphibolites and serpentinites at the expense of olivine rocks was related to a reaction of the ultrabasic melt with carbonate rocks, the undigested part of which has been preserved as xenolyths among the ultrabasic rocks of the massif.

The Khabozero intrusion of olivinites and pyroxenites has two phases of its formation. In the first, early stage fine-grained and medium-grained ore olivinites and pyroxenites segregated. The pegmatoid olivinites represent the second, later phase of segregation, since in the south-eastern part of the massif the author succeeded in observing xenolyths of fine-grained olivinite in pegmatoid olivinite.

The Khabozero deposit of olivinites represents a very rich raw material store for the refractory industry. Tests of refractory materials made at the Khabozero olivinite at the laboratories of the All-Union Institute of Economic Mineralogy (VIMS) in Moscow by A. S. Bazilevich (2) and in the Kharkov Institute of Refractories have shown that the Khabozero raw material is the best in the Soviet Union for substituting dinas in open-hearth and electric smelting furnaces. The reserves of a pure, nearly 100% olivinite reach tens millions of tons. Economically, the deposit lies under highly favourable conditions, since it is located at an elevated dry place, where cheap open-pit quarrying is possible.

The proximity of the Kirovsk railway main (6—7 km) and the line of high-voltage electric transmission further facilitates the organization of quarrying. The single and very serious difficulty in the development of the production of refractories on the spot is presented by the absence of local magnetite which is a necessary addition to the olivinite body.

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GENETICS

STUDIES IN GENETICS OF DEVELOPMENT. IV. FURTHER DATA ON THE SENSITIVE PERIODS IN DEVELOPMENT OF *DROSOPHILA MELANOGASTER*

By N. N. MEDVEDEV

(Communicated by N. I. Vavilov, Member of the Academy, 23. VIII. 1939)

The writer communicated in his previous papers that he had established on the basis of an analysis of 30 stocks of *D. melanogaster* the existence in the action of lethal genes upon development of special sensitive or critical periods, during which takes place the death of zygotes possessing unviability genes ([1],[2]). Such sensitive periods proved to be: embryonic development (i. e. the development of the embryo within the egg), the first instar of the larval life and the period which precedes pupation*. The processes of development which are taking their course at these stages appear to be in some way disturbed; the death of the zygotes possessing lethal genes is the result.

In the table below are presented data on the analysis of 18 other stocks of *D. melanogaster* possessing lethal genes; the analysis was conducted on the same scheme as that applied in the analysis of the preceding 30 stocks. The only difference in the method of the present experiments consisted in that females heterozygous for the lethal genes and belonging to the basic cultures were crossed with males of the Berlin-stock, in order to establish in two stocks the stage at which the lethal zygotes die during their larval period. Owing to this, there were somewhat different relations between the grey and yellow larvae produced by such females as noted in the table by corresponding footnotes (see columns 9,12 and 13).

Data of the table fully corroborate the observations which were made by us in the analysis of the preceding series of cultures. It appeared that in 8 out of the 18 stocks studied the death of the lethal larvae occurs during the pupal period of development. In the remaining 10 lines the death of the lethal zygotes falls to the embryonic or the larval periods of development, respectively. Among these there was found one culture characterized by the earliest manifestation of the lethal gene which kill the zygote already within the egg. In another culture the death of unviable males takes place at the adult larva stage (i. e. before pupation). Finally, in 8 cultures the death of the lethal larvae ensued at the first instar (i. e. at the period between hatching of larvae and the first moult).

The critical period of the action of the majority of lethal genes showing early manifestation thus proved to be confined to the first instar. Less

* Pupal lethals were yet subjected to detailed analysis neither in the present series of cultures, nor in the preceding one.

Summarized Data on the Analysis of the Stages at which Takes Place the Death of Unviable Zygotes in *D. melanogaster* Lethal Stocks

Stock No.[1]	Adult larvae found in the stock			Eggs			Larvae found in the stock during the larval development								Stage of death of the lethal males
							I instar		II instar			III instar			
									grey		yellow	♀♀	♂♂		
	♀♀	♂♂ yellow	♂♂ grey	Deposited	Did not develop	%	grey ♀♀ a. ♂♂	yellow ♀♀ a. ♂♂	♀♀	♂♂	♀♀ a. ♂♂	grey and yellow	yellow	grey	
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
A—3	110	14	110	—	—	—	—	—	—	—	—	—	—	—	Pupation
A—6	133	85	—	1 277	40	3.1	16 (6)	77 (63)	102 (100)	—	146 (131)	40 (37)	17 (14)	—	Larva, I instar
A—8	126	62	—	713	177	24.8	72 (66)	224 (192)	75 (74)	—	75 (67)	89 (83)	75 (66)	—	Egg
A—14	114	58	—	646	22	3.4	122 (55)	260 (218)	151 (138)	—	181 (162)	90 (87)	69 (60)	—	Larva, I instar
A—15	258	102	74	—	—	—	—	—	—	—	—	—	—	—	Pupa
Ca—1	121	66	—	950	42	4.4	118 (40)	117 (90)	92 (89)	—	153 (133)	234 (209)	95 (80)	—	Larva, I instar
Ca—3	54	32	143	—	—	—	—	—	—	—	—	—	—	—	Pupa
Ca—4	157	89	—	391	9	2.3	72 (14)	70 (59)	81 (77)	—	71 (58)	358 (320)	184 (159)	—	Larva, I instar
l^n—11	234	81	—	1 431	76	5.3	200 (51)	125 (109)	121 (109)	—	167 (146)	39 (37)	15 (10)	—	Larva, I instar
l^n—14	135	69	47	—	—	—	—	—	—	—	—	—	—	—	Pupa
l^n—15	155	54	34	—	—	—	—	—	—	—	—	—	—	—	Pupa
l^n—17	111	50	72	—	—	—	—	—	—	—	—	—	—	—	Pupa
l^n—20	250	125	14	—	—	—	—	—	—	—	—	—	—	—	Pupa
l^n—22	132	78	—	577	22	3.8	150 (39)	12 (11)[2]	218 (190	—	58 (48)[2]	92 (90)[3]	6 (6)	—	Larva, I instar
l^n—24	204	89	—	1 416	66	4.6	180 (101)	27 (20)[2]	172 (165)	—	91 (83)[2]	18 (18)[3]	13 (10)	—	Larva, I instar
l^n—25	236	84	71	—	—	—	—	—	—	—	—	—	—	—	Pupa
l^n— 2	323	225	—	1 311	51	3.8	302 (98)	126 (81)	104 (95)	—	139 (104)	39 (36)	10 (8)	—	Larva, I instar
l^n— 9	133	73	69	—	—	—	—	—	—	—	—	—	—	—	Pupa
Berlin	—	—	—	875	23	2.6	—	—	—	—	—	—	—	—	Control

[1] V. V. Sakharov's numeration of the cultures (the first 8 cultures, spontaneous point mutations) and that of M. L. Belgovsky (the remaining 10 cultures containing lethal genes obtained in experiments on ultra-violet rays; not studied cytologically); V. V. Sakharov and M. L. Belgovsky kindly put at our disposal their cultures for the present study. [2] Only ♂♂; explanation in the text. [3] Grey only: explanation in the text.

distinct are the two other periods, viz., the egg- or the embryonic period and the period which immediately precedes pupation.

A very characteristic feature of the sensitive periods consists in their distinctness in time: in none of the instances of larval or egg lethals studied by us was the death of the unviable embryos drawn over a long period of time; on the contrary, the development of all the unviable zygotes always stopped at the same strictly definite stage characteristic of a given stock, and besides, although such larvae could remain alive during a very long time (see below), their further development nevertheless ceased altogether.

It is somewhat premature to discuss the immediate causes of the death of unviable embryos; however, a number of observations make it possible to assume that inability of further development, of the larval lethal zygotes in particular, may be connected, in some of the cases at least, with the disturbance of such processes as moulting and pupation of the larvae. The following data and considerations speak in favour of it: 1) The possible common nature, in some larval lethals at least, which may be deduced from the fact, that lethal larval genes in the great majority of cases are manifested in larvae of the I instar and at the moment prior to pupation. 2) Similarity of behaviour in a whole series of stocks of unviable larvae, as shown by their inability to undergo the next moult or pupation and by the fact that they may remain at the corresponding sensitive stage as long as 8 and even 10 days. 3) Possibility of experimental prolongation of the development of such larvae to a certain extent which follows from Hadorn's data ([3]) and from our preliminary observations on rearing unviable larvae in a medium, to which ground normal larvae were added.

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GENETICS

NEW DATA ON THE ORIGIN AND TAXONOMY OF CULTIVATED CARROT

By P. ZAGORODSKIKH

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The culture of carrots dates back to ancient times and has been known for over 2000 years. The authors differ in the explanation they give to the history of this culture. Such investigators as Braun (1842), Gordon (1848), Krause (1904), Baur (1924), Thellung (1926), Rasmusson (1926), Komarov (1931) and others have maintained and proved that cultivated carrot owes its descent to hybridization processes only, and mainly to intercrossing of wild species. Other investigators—Hoffmann (1816), Vilmorin (1886), Rubashevskaya (1931) etc.—believed the cultivated carrot to have derived directly from the wild one, by selection and culture over a long period of time.

As a great variety of carrot forms were studied, the origin of cultivated carrot came clearer to show. It may be considered as an established fact that the cultivated carrot includes several extensive groups of various descent, the very process of their introduction into cultivation being likewise of varied nature.

The progenitors of cultivated carrot are forms of wild carrot. This extremely polymorphic species had in times prehistoric, as it has now, a rather wide range of distribution. The history of its culture shows that the most ancient group of cultivated carrot is the anthocyan carrot which is known to be most widely spread in Middle Asia and particularly rich in forms (in the easternmost region of South-Eastern Asia) at the junction of the mountain ranges of Hindu-Kush and the Himalayas (Afghanistan). N. I. Vavilov regards this region as the original home of the formation of cultivated carrot.

The process of cultivation of this group of carrot followed directly the path of improvement of wild forms with the assistance of man through centuries, at the beginning as a medicinal, and then as an esculent plant. This may be attested by experiments of Hoffmann, Vilmorin, Rubashevskaya and others, who succeeded within a short time by applying agricultural technique to raise wild forms to the rank of nearly cultivated ones. This is supported also by the fact that the roots of wild Asiatic carrot with a white colouring surface, when pulled out, assume anthocyan colouring after a few days' exposure to light, which is a phenomenon not observed in European wild carrot. Besides, there are some forms which, having the underground roots coloured white, show at the same time aerial parts of the root coloured violet. Thus, it is this group of carrot which exhibits more readily and on a larger scale quantitative and qualitative changes of pigments.

The anthocyan carrot contains two types of pigments: anthocyanins and anthochlors. The prevalence in roots of anthochlorine pigments produces the yellow colouring of roots, while the predominance of anthocyan pigments is responsible for the violet or black colour of roots. The anthochlorine pigments, according to their physical properties, approach the anthocyan pigments and precede their appearance in carrot roots.

With the appearance of anthocyan carrot in Middle Asia begins its natural hybridization with local wild forms. As a result arise forms having the surface and flesh of the root of pink and other colours; in all cases such roots contain anthocyan and anthochlorine pigments.

It should be noted that this group of carrots by their essential characters bear more likeness to the wild forms of the Asiatic carrot than other groups do. Plants of anthocyan carrot are characterized by light dissection of leaf blades, greyish-green leaf coloration, strong pubescence of the stems, the presence of anthocyan pigments in the cell sap of the root, a small core, a shorter vegetation period and a number of other characters. This group has been classed by us as subspecies (ecotype) of the Afghan carrot—subsp. *afganicus* m.

The range of the Afghan carrot is rather wide and extends all over Asia, Africa, and partly Europe. It migrated to Europe by two routes. One led via India and Fgypt, thence the carrot was transferred by moors to Morocco, and later to Spain. The second pathway led via Iran, Turkey, whence it was introduced to the Balkan peninsula. It reached Japan via China.

During one of its migrations the Afghan carrot penetrated into the semi-desert regions of Syria; the conditions of drought which prevail there affected essentially the nature of the plant for a rather considerable length of time. Thus, for instance, the rosette leaves of carrot became here covered with very densely set long soft hairs, imparting to the leaves a dove-grey tint. The roots roughened, but grew more drought-resistant (xerophile group).

Owing to such sharp distinctions of the basic characters of plants of this group from other groups of carrots, we have isolated the former in an independent subspecies of the Syrian carrot—subsp. *syriacus* m. The area of distribution of the Syrian carrot extends over Syria, Palestine, Irak, Iran and a considerable part of Africa.

Along the other route of the Afghan carrot extending from Middle Asia to Europe, it occurs in Asia Minor alongside of the here wide spread wild species of carrot *Daucus maximus*. At the place where these two forms of carrot met, they underwent hybridization. As a result, new forms arose bearing characters of the cultivated Afghan carrot and wild *D. maximus*, and those intermediate between them.

Special consideration should be given to forms wide spread on the Cilician elevation, characterized by giant development of rosette leaves, umbels and other aerial parts of the plants. The yellow and white colour of the roots of the Cilician carrot is due to the presence in the roots of anthocyan and anthochlorine pigments and even small quantities of carotene and lycopenoid pigments. These peculiarities of the Cilician carrot fully warrant its separation as an independent subspecies—subsp. *cilicicus* m.

The birth-place of the red, yellow and white carrot, widely spread in Europe, is the Mediterranean. Here flourished in times widely remote from ours the Greek and Roman culture with their highly developed agriculture, and undoubtedly, the Afghan carrot which migrated thither from Middle Asia, was at that time already under cultivation. Furthermore, here are concentrated the greatest numbers of wild species and subspecies of carrot which are closely related to one another, sometimes to such a degree that it is difficult to draw a demarcation line between them. The above may serve

as cumulative evidence that on the coast of the Mediterranean were evolving complicated and intensive form-building processes. As a result the greatest variety of forms of the group concerned is to be observed there.

Of this group of carrot the most ancient is the one with white coloured root surface ; the cultivation of this carrot, as well as of the Afghan anthocyan variety, proceeded by way of direct improvement of wild European forms with the assistance of man which lasted for centuries. As soon as it comes under cultivation, it is included into the general cycle of natural crosses with wild and cultivated Afghan forms. As a result appears a variety of carrot having the surface and flesh of the root coloured yellow, but as distinguished from the yellow Afghan variety it lacks anthocyan pigments, containing but anthochlorine and partly carotene pigments, formed as a result of biochemical processes occurring in the root cells, from primary carotenoids found in the wild European carrot.

The European yellow carrot differs sharply from the Afghan yellow one in the dissection, colouring and pubescence of the rosette leaves. As soon as the yellow carrot appears, it enters the general cycle of crosses with wild and cultivated white, and perhaps with the Afghan carrot as well. As a result the carotene red carrot appears, namely: its roots contain carotene pigments, the latter occurring in the cell plastids, and not in the cell sap, as it is observable in the Afghan carrot in respect to anthocyan and anthochlorine pigments. Thus, of the Mediterranean group of carrot the first to undergo cultivation was the one with the white coloured root-surface, the yellow one following next, while the red carotene carrot was the last one produced. All of this group of carrots are characterized by strongly dissected leaf blades, light and dark colouring, tender and succulent roots. The red colour of the roots is due to their containing carotene pigments in the plastids of the cell; the red carrot roots are distinguished by a high content of vitamin A, while in the carrot with white coloured roots it is practically entirely wanting. On account of the sharp and distinct characters this group of carrot was separated into an independent subspecies (ecotype) of the Mediterranean—subsp. *mediterraneus* m. This subspecies has a wide range, spreading throughout Europe, America, penetrating into Asia and Africa, where it is gradually replacing the Afghan violet carrot.

The carotene carrot was introduced into the Japanese islands, where the Afghan carrot was already widely spread by that time.

The mode of occurrence of these two groups of cultivated carrot on the Kyusyu island leads to their intercrossing with each other, as a result appear forms with blood-red coloration of the surface and flesh of the root caused by the presence of lycopenoid pigments. Conditions of high humidity prevailing in Japan and the deep tillage of soil by hand were favourable for the development of very long roots attaining sometimes 1 m in length. This group of carrot we have isolated into a subspecies—subsp. *japonicus* m.

The Japanese subspecies has a small area of distribution ranging mostly over the Japanese islands, occurring also in small numbers on the coast of the Japanese Sea.

According to the long accepted classification, the cultivated and wild carrot were representatives of one species established as early as by Linné (1753) as *D. carota*. Hoffmann (1791) was the first to separate cultivated carrot as a variety of the species *Daucus carota* L. (var. *sativus*).

As material was accumulating, cultivated carrot ceased to fit into the Hoffmann variety; therefore Hayek (1910) raised it to a higher taxonomic rank, i. e. to the subspecies *D. carota* L. subsp. *sativus* (Hoffm.) Hayek.

The wild carrot was likewise classed by Hayek under the subspecies *D. carota* subsp. *carota* Hayek. During the last decade, the subspecies of cultiva-

ted carrot subsp. *sativus* was differentiated into two large groups—the European and Middle Asiatic carrot. And now, since the new large groups of cultivated carrot—the Syrian, Cilician and Japanese—with those previously separated—the Afghan (Middle Asiatic) and Mediterranean (European)—have been described, the cultivated carrot together with the wild one present a quite composite complex which does not fit within the Linnean species *D. carota* L. Hence the question has naturally arisen as to the separation of cultivated carrot into an independent species, and that is exactly what we did, naming it *Daucus sativus* (Hoffm., Hayek) Zagor.

The wild carrot, accordingly, having retained its name *Daucus carota* L., should likewise be classified as a large independent species. Thus, the cultivated carrot species *D. sativus* Zagor. is differentiated into 5 groups which we have raised to the rank of subspecies (ecotypes) of cultivated carrot: 1) *D. sativus* subsp. *afganicus* Zagor.—Afghan carrot; 2) *D. sativus* subsp. *syriacus* Zagor.—Syrian carrot; 3) *D. sativus* subsp. *cilicicus* Zagor.—Cilician carrot; 4) *D. sativus* subsp. *mediterraneus* Zagor.—Mediterranean carrot; 5) *D. sativus* subsp. *japonicus* Zagor.—Japanese carrot.

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PLANT ANATOMY

OUTER INTEGUMENTS OF THE WHEAT KERNEL AS A CONDUCTING SYSTEM

By A. A. ALIAVDINA

(Communicated by A. A. Richter, Member of the Academy, 4. X. 1939)

While studying the structure of the integuments of the kernel of wheat, one comes to a conclusion that the anatomical structure of the various layers of the pericarp is characteristic of their conductive activities.

In my first work on the anatomy of the integuments of the kernel of wheat I have already ventured the opinion that the inner layers of the pericarp at least, i. e. the transversal and cystoid cells, must be endowed with conductive functions; the vertical flow passes through the cystoid cells, and the horizontal flow—through the transversal ones. The structural peculiarities of these layers first noted by me in *Tr. vulgare*, were later on observed on other material (*Tr. durum*, *Tr. monococcum*, etc.). These peculiarities in the first place are the following: 1) presence of pores in the contiguous walls of the cystoid cells (inner epidermis of the pericarp); 2) presence of pores also at the points where cystoid cells join the transversal ones; 3) lack of thickening or merely a slight thickening of the radial walls of the transversal cells; 4) development of structures resembling spiral thickenings in the most extended transversal cells, etc.

It was noted in earlier literature ([3]) that the cystoid cells show pores at the points of their junction with the transversal ones. The same was observed in *Tr. vulgare*, too. However, Alexandrov denies in his works the existence of the above pores ([1,2]).

The study of the pericarp carried out by me on several wheat species did not only confirm the existence of pores between the transversal and cystoid cells, but gave a clearer idea of their peculiarities which heretofore remained obscure.

One often happens to observe on cross-sections pores in the walls of the transversal cells above the cystoid ones (Fig. 1,*1*); however, no correspondingly localized pores could be detected in the cystoid cells on these sections. One gets an impression as if the cystoid cells were totally lacking pores in their outer walls, or as if the pores were situated here in no correspondence to their localization in the transversal cells. A detailed study helps to clear up this puzzling situation.

Fig. 1,*2* represents a surface preparation of the transversal and cystoid cells, as seen under the microscope focussed at different levels. When the higher level is focussed (Fig. 1, *2*,*a*), one may well see the walls of the transversal cells which lie above, while only the outlines of the underlying cystoid cells are to be seen. At the same time, one can easily observe the elongated

pores which cross the transversal cells, whereas only dim contours of other pores which cross the former are to be distinguished. When the microscope is focussed at a lower level (Fig. 1, *2,b*), the contours of the transversal cells become dim, as well as the pores situated across them; on the contrary, the outlines of the cystoid cells are well distinguishable, and the cleft-shaped pores situated across the cystoid cells become clearly manifest. The cleft-shaped pores are obviously situated both in the transversal and cystoid cells in the same manner as in other material, i. e. across the cell or somewhat obliquely. Inasmuch as the transversal and cystoid cells intersect, the direction of the pores cannot coincide in them. The connexion between the transversal and cystoid cells is effected not along the whole length of the pores, but only at the points of their intersections. It is obvious that, owing to such a localization of the pores, cross-sections would more often dissect the pores of the transversal cells, and this will be much rarer in the case of the intersecting pores of cystoid cells. This accounts for the somewhat unusual aspect shown by the Fig. 1, *1*. The localization of the pores is especially well seen on isolated cells and cell layers. In Fig. 1,*3* are represented several transversal cells (incomplete ones) and an end of a cystoid cell, from which an identical cell was detached; one may see that the latter was situated above the pore-bearing regions of the transversal cells. Fig. 1, *3,b* represents a fraction of an isolated cystoid cell with the pores.

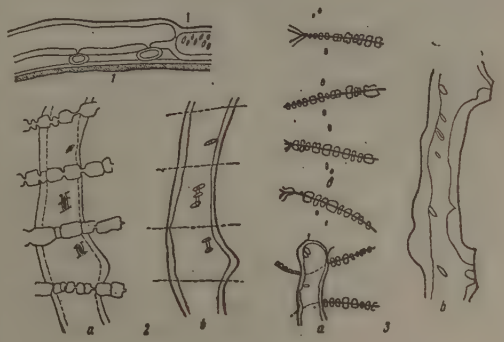

Fig. 1.

Sometimes there occur rounded pores at the points of junction between the cystoid and transversal cells; it becomes especially clear then, that they are bordered (Fig. 2, *4*). It is probable that in such cases the pores fully coincide possibly in cells of the two kinds.

Cystoid cells are sometimes connected with the transversal ones end to end (Fig. 2,*5*). No partitions can be distinguished at these points. It is possible that there is a clear connexion between the adjoining cells.

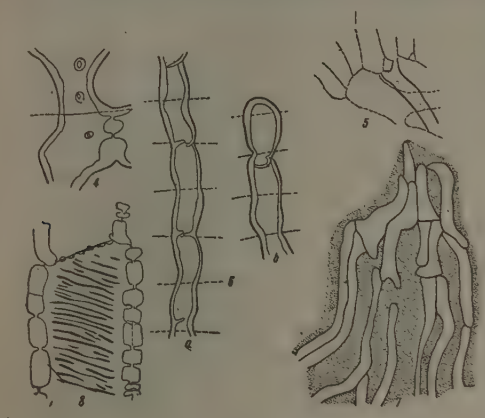

Fig. 2.

Transversal and cystoid cells are very firmly connected with one another; upon treatment with alkali they become, as a rule, detached as a whole from all the other pericarp layers and from the seed coat. The strips of cystoid cells running along the dorsal and ventral sides of the kernel are connected with the transversal cells (which form an uninterrupted layer) to fuse with them into a unit system.

Cystoid cells sometimes attain 650 μ in length and 10—15 μ in diameter.

It is possible that in some cases they are formed in the same manner as vessels. In favour of this is the fact that in the cystoid cells structures are sometimes found which may be interpreted as remnants of the transversal partition-walls (Fig. 2,*6 a* and *b*). The dorsal and ventral strips of cystoid cells broaden at the ends of the kernel and form caps which cover the base and the apex of the kernel. At these places the cystoid cells gradually fuse together (the apex of the cap), the connexion of cells remaining intact. The peculiar mode of connexion between the cystoid cells is especially manifest at the apical end (Fig. 2,*7*), and those cells which are located higher remind in shape and position the collecting cells of the mesophyll.

In outer layers of the pericarp, the epidermis (the outer one) and the parenchyma consist of cells drawn in the direction of the length of the fruit. Their longitudinal walls are strongly thickened and supplied with pores which in the epidermis often have the character of the bordered ones; the cross walls usually remain thin (Fig. 2,*8*). The epidermal cells at the basal end are drawn in length and become pointed like tracheids. Cleft-like pores may be sometimes detected in the inner walls of the epidermal cells. The thickening of such walls assumes the character of a step-thickening. Fig. 2,*8* represents a part of an epidermal cell with a step-thickening (from the apical end of the kernel). The outer walls of the epidermis always show a thickening. The above peculiarities of the structure of the outer layers of the pericarp should obviously also be accounted for by their conductive functions.

All the data contained in the present communication support and extend the idea of the pericarp in wheat as being a kind of a conductive system.

The results of the physiological experiments on the permeability of different parts of the kernel for solutions become intelligible in this connexion.

It is known from the literature ([4]) that when the kernel is immersed by either end into I—IK solution, the staining of the endosperm always begins at the region adjoining the embryo. I myself was able to verify these data. When kernels were immersed by the apical end into a sand wetted with I—IK solution, the region of the endosperm above the embryo became blue first, whereas the submersed apical portion of the endosperm remained entirely stainless.

It may be concluded from this that the apical end is permeable for the I—IK solution. It is obvious that it penetrates through the place where formerly the stigmata were situated, as well as through the region of stomata at the ventral side of the apical end. The solution enters from the apical end only into the pericarp, without penetrating at this point through the seed coat into the kernel, as shown by the experiments. One should think that the cuticle which isolates the pericarp from the seed coat and is formed (following literary data) through fusion of three cuticular pellicles, is impermeable for the I—IK solution. The solution passes by the conductive system of the pericarp to the basal end (where the embryo is found) and only here it enters the kernel.

Such a way of the water flow through the embryonic zone should be taken to have some advantages at the period of germination. Owing to this, may be controlled the water supply into the kernel, as well as the rate of dissolution of the endosperm materials in the course of the development of the embryo.

The conductive system of the pericarp in wheat seems also to participate in the transportation of plastic materials into the inner parts of the kernel during the period of ripening of the grain.

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PLANT PHYSIOLOGY

CONTRIBUTION TO THE STUDY OF CAUSES OF DEATH IN ROOT CROPS SUBJECTED TO LOW TEMPERATURES

By M. F. BUGAEVSKY

(Communicated by N. I. Vavilov, Member of the Academy, 21. IX. 1939)

It is known that on breaking or cutting frozen fleshy root crops (carrot, beet and others) one can easily see, even with the naked eye, ice formations of various size and shape firmly deposited in tissues. These ice formations produced by the freezing of tissue water often look like lenses. On thawing such root becomes flabby, easily gives off water and is unable to produce shoots. When defrosting the congealed root in ethyl alcohol (as a fixing fluid), one can see in sectioning its cavities where the ice was deposited.

To explain the causes of death of root crops Müller-Thurgau advanced a theory which gives this phenomenon the following interpretation. Originally in the intercellular spaces appear small crystals, then they swell at the expense of water adsorbed not only from the cells surrounding the intercellular space, but from more distant ones as well. As a result the protoplasm of the cell looses water, coagulates and dies. The ice crystals expanding in the intercellular spaces at the expense of water drawn from the cells, push the cell walls apart as if with a wedge, enlarging the intercellular spaces. As a result of freezing a number of root crops show rather long cavities formed by such accumulations of ice.

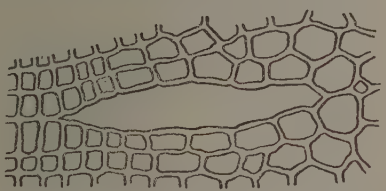

Fig. 1. Cavity in the carrot root formed as a result of disruption of cells by the accumulated ice, according to Müller-Thurgau.

To illustrate the above phenomenon in the freezing of roots we present a figure from the work of Müller-Thurgau (Fig. 1) ([1,2]). This is exactly how the process of freezing of fleshy root crops has been hitherto described both in monographs on frost-resistance of plants and agricultural text-books for colleges. «The cause of the death of a plant from frost is to be looked for in the change of the protoplasm, namely in its coagulation. And this coagulation is due to that the growing ice crystals in the intercellular spaces absorb water from the cells, the cell-sap becoming more and more concentrated, while the protoplasm loses more and more water» ([4]).

A similar explanation gives Molish who adds: «At the same time it is quite possible that sometimes the freezing of plants is caused by other agencies, too. A more exact analysis of the factors in question is still lacking»([5]).

However, on the basis of our cytological investigations of the causes of death of winter wheat from low temperatures, we believed that the explanation of the phenomena involved in the freezing of succulent roots deserves a different approach, and it would imply a different concept of the process of freezing and the causes of death of succulent root crops at low temperatures.

The reason why ice crystals may separate cell walls can be explained by the physical property of water to expand upon freezing. However, it remains unclear what are the forces drawing the water from cells to the ice crystals formed in the intercellular spaces, the former expanding to such an extent as to exert pressure against the surrounding cell walls, and just why the expanding ice crystals separate so regularly the cell walls. To study this phenomenon we carried out a number of experiments.

As material of investigation were used fresh root crops: *Daucus carota*, *Beta vulgaris*, *Raphanus sativus*, tubers of *Solanum tuberosum*. Microscopical studies (7) of the process of freezing of sections from the tissue of the fresh root of carrot showed conditions almost similar to the process of freezing of the tissue of winter wheat: ice film on the surface of the section plane, still before the ice formation in the cell. The cells of the carrot tissue passed the freezing period; with a further drop of t^0 ice formation ensued, and the cell protoplasm was ruptured by ice crystals in portions of various size.

Like in the experiments with winter wheat (7), one could see folds developed on the cell membranes due to the presence of ice crystals expanded in the cell at a temperature of about —10°C. Inasmuch as these observations were carried out on sections, and this did not fully reflect the actual process of freezing , we passed to the study of the freezing process in whole fresh roots, where according to the solidity of tissues the process of freezing assumes a peculiar course as compared to that of thin-leaved plants (winter wheat).

For our experiments whole roots of the above-mentioned plants were frozen to about—5°,—7.8°,—9°,—12.5°C. In some cases they were exposed to slow freezing, in others—to quick freezing, and at the same time sampled out for analyses. With the decrease of temperature, as soon as the freezing point is reached, ice formation ensues in the cell: thus, the freezing of tissues begins. When freezing fleshy roots, the physical properties of water should likewise be taken into consideration.

Distilled water is known to have its smallest volume at+4°C; with the raise or drop of temperature water expands. On freezing, i. e. passing into a solid state, water expands by 10% of its volume. If water is frozen in a closed vessel with very solid walls, it develops a pressure which may be expressed in terms of thousand of atm. per 1 cm^2. On free freezing of water the pressure is zero, since in this case the resistance of walls of the vessel is lacking.

Water being the indispensable component of a living cell fills all living tissues of a fresh root, except the intercellular spaces. With the beginning of ice formation the volume of each congealing cell increases at the expense of the water freezing in it, and as a result pressure increases in the freezing tissues, the intercellular space being unable to hold the additional volume of frozen water. In the tissues of thin leaves no such tension was observed, the thickness of their tissues, as compared to that of the fleshy root, being very small, while the cavities of the intercellular spaces are relatively large (7).

The freezing of the tissues of the carrot root begins on the periphery, whereby the still unfrozen inner portion of the root tissue seems to be hermetically enclosed from all sides in a tight fitting membrane of frozen tissue. This freezing layer thickens and penetrates farther and farther to the center of the root. With the thickening of the freezing tissue and a greater and greater amount of water changing to ice, the unfrozen tissue inside the root is subjected to the pressure of the freezing water. When later, with further freezing of water, the rate of pressure passes beyond the elastic limit of the frozen tissue, the latter is breaking down. As soon as the ruptures appear, water leakage ensues from the adjoining internal still unfrozen portion of the tissue. In case the rupture forms at an appreciable distance from the freezing layer, where the water is not likely to enter rapidly, such cavities

may gradually fill with crystals, whereby something like a lens consisting of grown together crystals is formed in the cavity. Such crystal patterns were observed by Müller-Thurgau (1). The pressure developed in some part of the still unfrozen area of the tissue as a result of the rupture of completely frozen tissue is for a moment released. Ruptures do not occur instantaneously.

The fact that the tissue is being disruptured in many places is due to the freezing substance, being a structure of the kind giving no free pathway for the movement of fluid. Hence with the rupture of tissue in one place, the pressure decreases but in the adjoining tissue, and not throughout the whole volume, where high pressure is operating. Within the remaining volume, where high pressure is also present, local ruptures of the same kind occur. Thus, in various places of the already frozen tissue ruptures are successively taking place, until the entire root is completely frozen, whereby not the whole amount of water in the cell is being frozen at once. The freezing of water in a living plant cell depends upon the time, temperature, quality and quantity of the cell contents. The lower the temperature, the greater the amount of water freezing up in the cell and the greater the size of the ruptures eventually forming.

The cracks within the tissue of the carrot root are not irregularly disposed, a regularity being apparent in their arrangement with respect to the form of the root. In the peripheral tissue of the frozen root cracks are arranged in concentric rings, and further away from the periphery the cavity fissures of the root assume a radial arrangement, thus running to the center of the root. In a number of other instances none of this regularity in the arrangement of the cavity cracks in the tissue is observed for the reason indicated below.

The pressure exerted by the freezing water within the tissues inside the root of carrot, beet, etc., is apt to develop to such an extent, that on the fresh succulent root, along with the cracks within the tissue and the small fissures in the peripheral tissue, a large deep external crack may be formed extending longitudinally over the root.

Besides the cavities where ice had been accumulating, which may be observed with the naked eye, there were cavities of microscopic size. In fact a picture very characteristic of all the cavities is thereby revealed. On microscopical examination practically all the walls of the cavities present an uneven mellow disrupted surface. Almost all the walls of the cavities exhibit distinctly ruptured portions of the tissue of various size and shape or disruptured cell membranes. The cell content from such disrupted cells often empties out into the cavity. In the cells which remained intact the dead matter of the cell may be seen in the form of one or several free clots. As a rule, such was the appearance of cavities commonly observed (Fig. 2).

Ruptures of the kind indicated by Müller-Thurgau, where cell walls were separated by the ice without disrupting the cell walls proper (Fig. 1), came rarely under our notice; this phenomenon we regard as incidental.

We were freezing root crops previously sliced by a razor blade into sections of different size, both in length and in thickness. The thinner the section treated, the smaller were the cavities. Sometimes the sections were so thin, that no cavities were forming, for in thin sections on freezing no such pressure could develop which would deform the frozen tissue of the root, since part of the water of the given section, as compared to the whole root, gathered on the surface and froze, whereas the remaining amount of water began to freeze within the cells proper.

When thoroughly freezing roots killed (with alcohol, hot steam, chloroform), we observed the same regularity in the arrangement of the cavities formed, as on freezing living root. When flaccid roots (carrots and other succulent plants) were frozen, no external deep cracks occurred whatever,

there were none of the external cracks in the peripheral tissue extending along the tangent direction either, as observed by us in fresh roots. The more flaccid the root, the less was the number of cavities formed within. Depending upon the degree of flabbiness, there were areas in the tissue which contained no cavities whatsoever. A fresh potato tuber on freezing did not produce such a great number of cavities as compared with fresh carrot roots. There were such potato tubers which showed no cavities on freezing. Large areas of the tissue of potato tuber showed no cavities since the cells filled with starch grains contained little water; consequently, in those areas no such high pressure could develop which would rupture the frozen tissue.

The freezing of a fresh succulent root is not as simple a process as in some homogeneous medium. The direction and value of pressure and hence the direction and size of cavities in the root tissue are affected not only by the amount of water contained in the roots, but likewise by the structure of the tissue and rigidity of cell walls which vary depending upon vital functions of the root tissues, to say nothing of the cell contents, whose qualitative and quantitative composition is of prime importance at the tissue freezing.

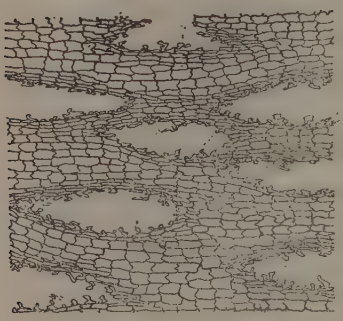

Fig. 2. Cavities in the carrot root formed as a result of the rupture of tissues under pressure developed in the freezing of the root.

Conclusions. On freezing of succulent roots (carrot, beet, etc.) the formation of cavities within the tissues is a result of their rupture by pressure developing in tissues on freezing of the tissue water.

The walls of the cavities forming in tissues, while the latter are freezing, display a loosened surface where ruptured cell membranes and portions of membranes are gathered, and parts of the disrupted tissue are sometimes suspended.

On freezing of succulent root crops (carrot, beet, etc.) and potato tubers, the death of the living cell protoplasm may be the result of: 1) its rupture by ice crystals forming inside the cell; 2) mechanical pressure; 3) injury during the rupture of the cell membrane.

Thus, it is wrong to explain the destruction of protoplasm on freezing of succulent roots (carrot, beet, etc.) as caused by dehydration due to the withdrawal of water from cells to intercellular spaces, and hence explanation of the formation of cavities within the frozen rootis equally wrong.

As there are plants which die also from dehydration of the protoplasm, for instance, the classical object *Spirogyra* (weeds) ([1]), a differential approach to the explanation of the process of destruction of various plants and their organs by frost is necessary.

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EXPERIMENTELLE MORPHOLOGIE

ÜBER DEN BEGRIFF DER POLARITÄT DER KONSTITUTION IN DER EXPERIMENTELLEN MORPHOLOGIE

Von J. SCHAXEL und T. IVANOVA

(Vorgelegt von I. I. Schmalhausen, Mitglied der Akademie, d. 17. X. 1939)

Der Ausdruck «Polarität» wird in der experimentellen Morphologie teils zur Beschreibung tatsächlicher Verhältnisse, teils zu ihrer hypothetischen Erklärung gebraucht. Im ersten Sinne besagt die Polarität der Zellen, Gewebe, Organe und Körper, dass bei Protisten, Pflanzen und Tieren sich deren einzelne Abschnitte bei Neubildungsvorgängen in der Richtung einer oder mehrerer Achsen verschieden verhalten. Beispiele solcher Art sind folgende: das ausgeschnittene Mittelstück des Infusors *Stentor* bildet apikalwärts ein Peristomfeld, basalwärts ein Fussende. Bei den Pflanzen gehen von den Vegetationspunkten des Sprosses und der Wurzel verschiedene Bildungen aus. Äusserlich ähnlich den Pflanzen verhalten sich die festsitzenden Coelenteraten (*Antennularia*, *Tubularia*, *Corymorpha* und andere). Bei bilateral symmetrischen Tieren (z. B. Planarien, Anneliden) spricht man von dem polaren Gegensatz des Vorder- und Hinterendes.

Die Untersuchung der Regenerationsprozesse nach Entfernung von Körperteilen ergibt, dass die Polarität nur relativ, besser gesagt, labil ist. Bei Pflanzenstücken, die mit dem Scheitel nach unten und mit der Basis nach oben in der feuchten Kammer aufgehängt werden, treiben die Vegetationspunkte am apikalen (jetzt unteren) Pol Wurzeln und am basalen (jetzt oberen) Pol Sprosse. Das abgeschnittene Köpfchen von *Tubularia* bildet an der basalen Wunde noch ein Köpfchen. Ähnliche Janusbildungen kommen bei Planarien vor. Die isolierten Hintersegmente des Regenwurms können nach vorne ein zweites Hinterende bilden. Das sind die sogenannten polaren Heteromorphosen. Sie haben die Autoren veranlasst, von gradueller (Child) oder mehrfacher (Fischel) Polarität, von Polaritätsumkehr (Voechting), von Apolarität (Loeb), von Heterotropie (Morgan) zu sprechen. Die labile Polarität ist auf jeden Fall keine Erklärung, sondern bestensfalls nur die Beschreibung eines wechselnden Tatbestandes.

Der methodologische Fehler aller dieser Erklärungsversuche ist ein zweifacher: erstens werden die Erscheinungen für sich isoliert und nicht im Zusammenhang der ontogenetischen Prozesse im Ganzen betrachtet, und zweitens wird nicht eindeutig klargestellt, was die Regeneration im Entwicklungsablauf eigentlich ist.

Der Versuch, die Polaritätserscheinungen durch eine Schichtung verschieden wirksamer Stoffe in den polaren Körpern, durch Verschiedenheiten der materiellen Struktur (Morgan, Przibram) oder durch bestimmt gerichtete

Nährsaftströmungen (Voechting, Pfeffer, Winkler) zu erklären, hätte viel für sich, wenn diese Annahmen bewiesen wären; aber das sind sie nicht. Wird im Gegensatz zu solcher «struktureller» oder «dynamischer» Polarität angenommen, dass es überhaupt keine endogene Polarität gebe und dass exogene Faktoren die sogenannten Polaritätserscheinungen hervorrufen (Loeb: Wirkung der Schwerkraft je nach der Lage im Raum bei *Tubularia*; M. Nussbaum: Wirkung der Nachbargewebe auf indifferente Regenerationskegel bei Anneliden), so wäre das ebenfalls zu beweisen.

Es liegt im Bereich der Möglichkeit, durch geeignete Versuchsbedingungen die Annahme der exogenen, dynamischen und strukturellen Polarität miteinander in Verbindung zu bringen. Schon 1891 hat W. Roux (2) versucht, durch elektrische Durchströmung bei Eiern und Embryonen morphologische Polarität zu erzeugen. Später haben andere, besonders E. Lund (1), aus den Folgen der Durchleitung des elektrischen Stromes durch Stammstücke von Hydroidpolypen Folgerungen gezogen. Lund erhielt je nach der Stromstärke am Kathodenende andere Bildungen als am Anodenende (Hydranthen- oder Stolonenbildung), unabhängig von dem ursprünglich apikalen oder basalen Ende der Stammestücke. Es liesst sich denken, dass der elektrische Strom eine Bewegung und Verlagerung formbildender Stoffe bewirkt, also «exogene» Faktoren die «strukturelle» Polarität herstellen. Die Schwierigkeit dieser Polaritätsannahmen liegt darin, dass über die Natur der «formbildenden», durch den elektrischen Strom verlagerbaren Stoffe nichts bekannt ist, und dass die elektrischen Ströme des Experiments in der Natur nicht vorkommen.

Im Gegensatz zu den widersprechenden Angaben über die Polarität von Körperstücken sind die Verhältnisse in den frühesten ontogenetischen Stadien eindeutig festgestellt. Im Falle des tierischen Eies pflegt die vergleichende Embryologie den animalen vom vegetativen Pol zu unterscheiden, um die verschiedene Rolle der Eiteile in der Entwicklung anzugeben. Die experimentelle Forschung hat diese «Polarität» sowohl in ihrer Entstehung, wie in ihrer Wirkung genau bestimmt. Wir haben dafür die Bezeichnung «Konstitution» eingeführt (4) und hinzugefügt: «Wenn wir im gleichen Sinn auch Polarität sagen, weil die Konstitution in keinem Falle eine in der Richtung aller Achsen gleichartige ist, so sei ausdrücklich betont, dass der viel missbrauchte Begriff der Polarität für uns weiter keinen geheimnisvollen Inhalt hat, sondern nur das jeweils besonders anzugebende Lageverhältnis der sichtbaren Teile zueinander umschreibt». Der aus der zytologischen Analysis der Entwicklungsvorgänge abgeleitete Begriff der Konstitution der Zelle (3) wurde 1915 folgendermassen auf die ontogenetische Determination angewandt: «Die in sich geordneten Teile, die in der Ontogenesis die typischen Bildungen zustande bringen, sind die Zellen. Ihre Ordnung ist ihre Konstitution. Als Konstitution bezeichneten wir die... Tatsache, dass die Zelle weder isotrop ist, noch eine unwesentliche Anisotropie aufweist, sondern von verschiedenen Komponenten in bestimmter räumlicher Zuordnung zusammengesetzt wird. Die Zelle ist weder eine gleichartige Masse, noch ein Gemisch beliebig verteilter Stoffe, sondern besitzt einen typischen Bau, in dem qualitativ differente Substanzen in bestimmter Quantität einander räumlich in bestimmter Weise zugeordnet sind. Diese Zuordnung ist keine starre, sondern eine elastische, so dass sie durch sich wieder ausgleichende Umformungen der Zelle, z. B. bei amoeboiden Bewegungen, keine Störung erleidet... Die Konstitution der Zellen ist die von allem Anfang der Entwicklung angegebene Ordnung des in sukzessiven Akten sich umbildenden Systems» (4). Der in 25-jähriger experimenteller Forschung weiter geprüfte und bewährte Begriff der Zellkonstitution bezeichnet die «Tatsache, dass in der Zelle qualitativ differente Substanzen regional gesondert, quantitativ verteilt und einander typisch zugeordnet sind» (6).

Die gegenwärtige Kenntnis des Verlaufs der ontogenetischen Determination schliesst den oben genannten doppelten methodologischen Fehler aus. Die Determination geschieht in sukzessiven Akten durch einander nachgeordnete Veränderungen materieller Teile, die in der Zellkonstitution, den Zellgebilden, ihrem gegenseitigen Lageverhältnis und ihren stofflichen Beziehungen samt ihren Produkten und Derivaten gegeben sind. Bei einer solchen Geschehensweise befindet sich jeder Faktor räumlich und zeitlich an der Stelle seines Wirkens. In den aufeinander folgenden Stadien ergibt sich das Zusammenwirken der Faktoren von Akt zu Akt aus der Konstellation der Teile. Die Formbildung geschieht durch örtlich, zeitlich, intensiv, quantitativ, qualitativ bestimmtes Teilungs-, Bewegungs-, Erzeugungsgeschehen. Als Bildner fungieren Zellen, Zellkomplexe und Zellderivate. Die Konstitution der Zelle ist eine vorläufige, aber wesentliche Etappe der analytischen und synthetischen Forschung. Die nächste Aufgabe ist die Erforschung der physikalischen und chemischen, zunächst der physikochemischen und biochemischen Natur der Zellkonstitution.

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EXPERIMENTELLE MORPHOLOGIE

EXPERIMENTELLE BEITRÄGE ZUR FRAGE DER POLARITÄT BEI DER REGENERATION

Von J. SCHAXEL und T. IVANOVA

(Vorgelegt von I. I. Schmalhausen, Mitglied der Akademie, d. 17. X. 1939)

Aus unseren Darlegungen über den Begriff der Polarität und Konstitution ([3]) geht hervor, dass die sogenannten Polaritätserscheinungen bei der Regeneration nur im Zusammenhang mit den gesamten ontogenetischen Prozessen betrachtet werden können. Im Anschluss an frühere Mitteilungen ([1,2,4]) berichten wir hier über neue Versuche mit Axolotln (*Siredon pisciforme* Shaw.) der weissen und schwarzen Rasse im Alter von 4 bis 7 Monaten (Länge 110 bis 150 mm), nämlich über die Versuchsgruppen A, B, C und D.

A) Exartikulation der Extremität und Implantation eines 4 bis 6 mm langen Stückes aus der Mitte des Oberschenkels in die Exartikulationswunde bei Erhaltung (a) und nach Umkehrung der Polarität (b).

a) Nach Anheilung erfolgt von der freien, distalen Wunde des Replantats aus Regeneration der distalen Partie. Die histologische Untersuchung ergibt, dass die Gewebe des Replantats teilweise erhalten bleiben und insofern in die Neubildung übergehen, als die Regeneration Sprossung von der Wundfläche aus ist.

b) Die Anheilung des Replantats das der Exartikulationswunde mit seinem ursprünglich distalen Ende aufliegt, erfolgt im Vergleich mit a) langsamer. Weiterhin ergeben sieh drei Grenzfälle:

1) Die freiliegende proximale Wundfläche des Replantats vernarbt. Darüber hinaus erfolgt keine Neubildung (Abb. 1).

2) Am freiliegenden Ende des Replantats erfolgt, im Vergleich zu 1) erheblich verzögert, eine mehr oder weniger atypische Regeneration. Die histologische Untersuchung ergibt, dass von den differenzierten Geweben des Replantats nur die Haut erhalten bleibt. Im Stadium der Regenerationsknospe umhüllt die Replantathaut von den inneren Replantatgeweben nur degenerierte Reste, die in indifferente blastemartige Zellmassen eingebettet liegen. Diese sind sum kleineren Teil durch die Vermehrung der indifferenten Reservezellen des Replantats entstanden, zum grösseren Teil aus den Wirtsgeweben unterhalb der Exartikulationswunde eingewandert. Die regressiven Degenerationsprozesse und die progressiven Regenerationsprozesse gehen zuerst nebeneinander her, bis dann diese über jene überwiegen. Auf die Einzelheiten der Gewebevorgänge kommen wir an anderer Stelle zurück. Die entstehenden Regenerate sind nach ihrer Determination völlig und nach ihrem Material hauptsächlich Gebilde des Replantatsempfängers. Die Regeneration geht vom Grunde aus unter Einbeziehung von Implantatmaterial vor sich. Vom

Replantat erhalten bleibt schliesslich nur die Haut, die die Neubildung proximal manschettenartig umhüllt (Abb. 2).

3) Die Anheilung des Implantats erfolgt in der Weise, dass einerseits die Implantatgewebe ernährt und zu Neubildungen befähigt werden, andererseits die Exartikulationswunde nicht völlig verschlossen wird und daher unmittelbar von hier aus Neubildungen vor sich gehen können. Es entstehen Regenerate in der Form von Doppelbildungen. Früher wurden in ähnlichen Fällen auch Drei- und Vierfachbildungen beobachtet ([2]). Bei heteroplastischer Transplantation (schwarzes Extremitätstück auf weissem Axolotl) sind die Doppelbildungen chimärisch (Abb. 3) und zeigen dadurch deutlich die

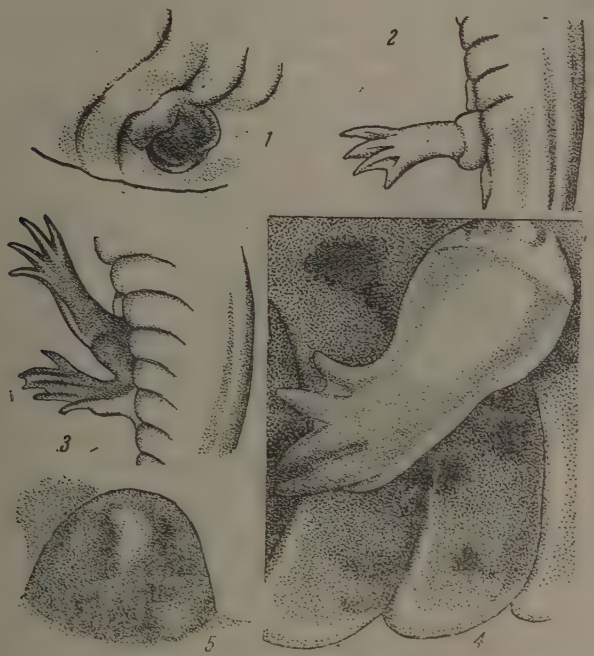

Abb. 1. Vernarbung des invertierten Replantats auf der Exartikulationsstelle.
Abb. 2. Regenerative Durchwachsung des invertierten Replantats auf der Exartikulationsstelle.
Abb. 3. Chimärische Doppelbildung nach heteroplastischer invertierter Implantation auf die Exartikulationsstelle.
Abb. 4. Regeneration des polaren heteroplastischen Transplantats auf den Rücken.
Abb. 5. Vernarbung des invertierten heteroplastischen Transplantats auf den Rücken.

Teilnahme von Material des Transplantats und der Unterlage an der Neubildung. Die histologische Untersuchung auf verschiedenen Stadien und im ausgebildeten Zustande klärt darüber auf, wie die differenzierten Gewebe des Transplantats mit Ausnahme der Haut zugrundegehen, ein starker Zustrom von Blastem aus dem Wirtskörper stattfindet, an zwei oder mehr Stellen Bildung von Anlagen und dann deren Differenzierung stattfindet. Die Mehrfachgebilde sind in sich selbständig (wie ihre atypischen Besonderheiten zeigen), insgesamt aber doch von der Unterlage aus determiniert. Vom Wirtskörper erfolgt auch ihre regenerative Innervation. Davon hängt wieder ihre spätere Bewegung ab.

B) Amputation der Extremität oberhalb des Kniegelenks und Replantation des Kniestückes auf den Oberschenkelstumpf bei Erhaltung (a) und nach Umkehrung der Polarität (b).

a) Nach Anheilung erfolgt an der freien, distalen Wunde des Replantats Regeneration der distalen Partie. Sie ist Sprossung von der Wunde aus. Alles entspricht den Vorgängen bei A (a).

b) Es zeigen sich keine wesentlichen Verschiedenheiten im Vergleich zu A (b). Die Replantatgewebe werden weitgehend zerstört, so dass eine abschliessende Vernarbung oder eine regenerative Durchwachsung der Replantathautmanschette vom Stumpf aus vorkommt. Auch Doppelbildungen werden beobachtet. Die Entstehungsursachen sind dieselben wie in A (b, 3). Alle Neubildungen sind nach Form und Umfang vom Oberschenkelstumpf aus determiniert und unterscheiden sich dadurch von der Kontrolle, wo stets die vom Implantat determinierte distale Partie (Unterschenkel mit Fuss) gebildet wird.

Abb. 6. Chimärisches formal unbestimmtes Gebilde nach invertierter heteroplastischer Transplantation auf den Rücken.

C) Amputation der Extremität oberhalb des Kniegelenks und Transplantation des Kniestückes auf den Rücken seitlich vom Flossensaum bei Erhaltung (a) und nach Umkehrung der Polarität (b).

a) Nach Einheilung wird an der Distalseite die distale Partie regeneriert. Da keine regenerative Innervation stattfindet, bleiben die qualitativ ausgebildeten Regenerate funktionslos und klein [Abb. 4; siehe auch (4)].

b) Nach Einheilung des Transplantats ergeben sich zwei Grenzfälle:

1) Im Transplantat gehen regressive Umbildungen vor sich, die mit der Vernarbung der freiliegenden Wundfläche enden. Es bleibt schliesslich ein kleines von der Haut des Transplantats umhülltes Restgebilde aus Narbengeweben übrig (Abb. 5).

2) Im Transplantat kommen nach anfänglichen Rückbildungsvorgängen progressive Umbildungen in Gang, die unter Teilnahme vom Zellmaterial, das aus der Unterlage stammt, zu unbestimmbaren Bildungen chimärischen Charakters führen (Abb. 6). Die Unterlage liefert zwar Material, determiniert aber nicht. Die eigene Determination des Transplantats kommt nach der Polaritätsumkehr nicht in Gang. Nur in einem Fall, wo das Transplantat nach Lockerung nur mit einem Stilchen der Unterlage aufsass, wurden Anfänge von Selbstdifferenzierung beobachtet.

D) Exartikulation der Extremität. Nach Resektion des proximalen (Oberschenkelstück mit Gelenkkopf) und distalen Endes (Fuss) wird das Extremitätmittelstück senkrecht zur Wirbelsäule in die Schwanzwurzel transplantiert. Durch ringförmige Entfernung der Haut am Transplantat wird die Einheilung ermöglicht. Wir erhielten Vernarbung an beiden freien Enden der Transplantate, möchten das Ergebnis aber deswegen nicht als endgültig ansehen, da bei einem früher ausgeführten Versuch Vernarbung des ursprünglich proximalen und Regeneration am ursprünglich distalen Ende des Extremitätstückes beobachtet wurde.

Ergebnisse. Bei polar implantierten Beinstücken des Axolotls erfolgt, unabhängig vom Implantationsort, Sprossung von der freien Wundfläche aus. Die Regeneration ist im Implantat determiniert (Versuche A, a, B, a,

C. a). Nach Anheilung invertierter Implantate findet, metaphorisch ausgedrückt, ein «Kampf der Teile» statt, der, je nach den Verhältnissen des Einzelfalls, entweder mit dem Unterbleiben einer Neubildung endet (Vernarbung; Versuche A, b, 1 und C, b, 1), oder nach weitgehender Zerstörung der Implantatsgewebe zur Regeneration von der Unterlage gemäss deren Determination (Versuch A, b, 2) oder bei fehlender Determination zu unbestimmten Gebilden (Versuch C, b, 2) führt, oder es kommen Mehrfachgebilde chimärischer Art gemäss der Determination der Unterlage zustande (Versuche A, b, 3 und B, b).

Die ontogenetische Determination ist ein zwangsläufiger Prozess. Da sie in sukzessiven Akten vor sich geht, kann sie durch äussere Eingriffe in neue Richtungen gezwungen werden. Das gegenseitige Lageverhältnis der Teile eines Gebildes, seine Konstitution, wirkt als Determinationsfaktor, gleichviel, ob das gegebene Lageverhältnis erhalten bleibt oder von aussen geändert wird. Ausser von der Konstitution noch von der Polarität zu sprechen, erübrigt sich. Etwas, was als «regulative oder gar finale Polaritätsumkehr» gedeutet werden könnte, kommt nach operative Umlagerung von Teilen nicht vor.

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EXPERIMENTELLE MORPHOLOGIE

ÜBER DIE BEDEUTUNG DES EPITHELS UND MESODERMS BEIM VERLUST DER REGENERATIONSFÄHIGKEIT DER EXTREMITÄTEN BEI DEN ANUREN

Von L. W. POLEŽAJEW

(Vorgelegt von I. I. Schmalhausen, Mitglied der Akademie, d. 5. X. 1939)

In meinen früheren Arbeiten ([3],[4],[5]) habe ich das Problem des Verlustes und der Wiederherstellung der Regenerationsfähigkeit der ganzen Extremitäten der Anuren studiert. Danach habe ich den Plan meiner Arbeit erweitert und vertieft, indem ich die Frage über die Bedeutung der einzelnen Teile der Extremitäten sowie des ganzen Organismus des Tieres bei den angeführten Erscheinungen aufstellte. Der normalen Ontogenese der Extremitäten entsprechend, haben wir es bei der Regeneration auch mit folgenden 4 Grundteilen zu tun: 1) dem Epithel, 2) dem Mesoderm, 3) den Nerven und 4) dem gesamten humoralen Mittel des Tieres. Über die Rolle des humoralen Mittels habe ich schon früher ([8]) berichtet, über die Rolle der Nerven werde ich ein anderes Mal besonders sprechen. In der vorliegenden Arbeit will ich die Versuche beschreiben, die zur Aufklärung der Rolle des Epithels und Mesoderms beim Verlust der Regenerationsfähigkeit der Extremitäten bei den Anuren dienen. Diese Versuche wurden mittels Verpflanzung des Gewebes von regenerationsfähigen- und regenerationsunfähigen Tieren vorgenommen: xenoplastisch, wenn die ersteren Urodela, die letzteren—Anura waren; und homoplastisch, wenn Anuren in verschiedenen Entwicklungsstadien genommen wurden.

Xenoplastische Verpflanzungen. Im Jahre 1935 wurden Haut und Mesoderm (Muskeln, Bindegewebe und Skelett) der Extremitäten zwischen erwachsenen Fröschen (*Rana temporaria*) und grossen Axolotlen (*Amblystoma mexicanum*) verpflanzt. Im Jahre 1938 wurde ein ähnlicher Versuch zwischen Kaulquappen (*Pelobates fuscus*) und Axolotlen vorgenommen. Nach der Verpflanzung wurde die chimärische Extremität im Transplantat amputiert. Die Versuche misslangen: die Transplantate fielen entweder ab, oder wurden vom Gewebe des Wirts verdrängt. Im Jahre 1936 wurden Verpflanzungsversuche von Epithel und Mesoderm der Extremitätsanlagen im Neurula-Knospenstadium an Tritonen, Axolotlen, *Rana esculenta*, *Bombina* und *Pelobates* vorgenommen und teilweise veröffentlicht ([6]), aber auch sie erwiesen sich im Grunde als misslungen. Im Jahre 1939 wurde eine grosse Anzahl (110 Versuche) Verpflanzungen von Extremitäten und deren Mesoderm und Epithel zwischen kleinen Axolotlen (2—4 cm lang) und Kaulquappen der *Rana temporaria* mit nachfolgender Amputation im Transplantat vorgenommen. Trotz des guten Anwachsens regenerierte die Extremität in

keinem einzigen Fall, und wurde das Transplantat von den Geweben des Wirts verdrängt.

Die Erfahrungen fünfjähriger (1935—1939) erfolgloser Arbeit haben mich davon überzeugt, dass das von uns gestellte Problem nach der xenoplastischen Methode nicht gelöst werden kann. Die biochemische Verschiedenheit zwischen den Geweben der Urodela und der Anuren, sowohl der vollständig entwickelten, wie auch der Larven, ist so gross, dass die Regeneration der Extermitäten und ihrer Teile bei xenoplastischer Verpflanzung stets gehemmt wird.

Homoplastische Verpflanzung. Der Versuch wurde im Sommer 1939 an Kaulquappen der *Rana temporaria* in folgenden Stadien vorgenommen: I Stadium—die Hinterextremitäten haben noch kein gegliedertes Gelenk zwischen Ober- und Unterschenkel, die Zehen sind noch zackenförmig. II Stadium—Ober- und Unterschenkel bilden einen stumpfen Winkel, die Zehenanlagen sind deutlich ausgebildet, die Extremitäten schwach entwickelt (IIa Stadium), oder gut entwickelt und grösser (IIb Stadium). III Stadium—Ober- und Unterschenkel sind stark entwickelt und bilden einen spitzen Winkel; der Bauch ist dick und gerundet, die Vorderextremitäten noch nicht bemerkbar (IIIa Stadium); oder aber ist der Bauch dünn, die Vorderextremitäten stehen unter der Operkularmembran hervor (IIIb Stadium). IV Stadium—die Vorderextremitäten dringen hervor. Laut unserer Angaben ([7]) regenerieren die Extremitäten bei Amputation im distalen Teil des Unterschenkels vollständig im Stadium I in 90.7% der Fälle; im Stadium IIa in 42.6%; sie regenerieren nur teilweise im Stadium IIb, und gar nicht vom Stadium III an.

Zur Aufklärung der Rolle des Mesoderms beim Verlust der Regenerationsfähigkeit einer Extremität wurde folgender Versuch angestellt. Einer Kaulquappe im Stadium IIIa wurde hart am Körper ein Hinterbein abgeschnitten, von dem die Haut abgezogen und dessen distaler Teil im Unterschenkel amputiert wurde. Das Mesoderm (Muskeln, Bindegewebe und Skelett) des Ober- und Unterschenkels wurde unter das Seitenepithel an der Wurzel des rechten Hinterbeins einer Kaulquappe im Stadium I verpflanzt. Auf diese Weise wurde in diesem Versuch (Serie U) das Mesoderm einer nicht regenerationsfähigen Extremität mit dem Epithel* einer regenerationsfähigen Kaulquappe kombiniert. Zur Kontrolle wurde folgender Versuch (Serie Tsch) angestellt, der zugleich auch Kontrollversuch für alle anderen Serien ist: das Mesoderm des Ober- und Unterschenkels (ohne Fuss) wurde autoplastisch unter das Epithel des rechten Hinterfusses einer Kaulquappe im Stadium I verpflanzt.

Zur Aufklärung der Rolle des Epithels beim Verlust der Regenerationsfähigkeit der Extremität wurden folgende Versuche angestellt, bei denen das Mesoderm regenerationsfähiger Extremitäten mit dem Epithel regenerationsunfähiger Extremitäten kombiniert wurde. Das Mesoderm des Ober- und Unterschenkels (ohne Fuss) im I Stadium wurde unter das Epithel des Unterschenkels einer Kaulquappe im Stadium IIb (Serie LIIb) oder Stadium IIIa (Serie LIIIa) verpflanzt. Diese Versuchsserien hatten den Fehler, dass das Mesoderm des I Stadiums nicht nur die Wirkung des Epithels der Stadien LIIb oder LIIIa empfand, sondern auch die Wirkung des humoralen Mittels dieser Stadien, die den Regenerationsprozess hemmt ([1],[2],[8]). Darum wurde noch eine Reihe von Versuchen vorgenommen (Serie C). Kaulquappen im I Stadium wurde die Haut der Extremitäten der Stadien IIIb—IV auf den Rücken verpflanzt, und 24 Stunden nach der Anheilung

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* Die den Versuchen unterworfenen Kaulquappen hatten auf ihren Extremitäten und an der Seite keine Haut, sondern nur Epithel und Basalmembran.

wurde das Mesoderm des Ober- und Unterschenkels (ohne Fuss) von Extremitäten des I Stadiums autoplastisch unter die verpflanzte Haut (in die Mitte derselben) verpflanzt. Auf diese Weise wurde das Mesoderm des I Stadiums und das humorale Mittel der Kaulquappe des I Stadiums mit dem Hautepithel der Extremitäten in den Stadien IIIb—IV kombiniert.

In all diesen Versuchsserien wurde ein unbedeutender Teil des aussen befindlichen Mesoderms im Lauf von 24 Stunden von dem es umgebenden Epithel bedeckt, und wurde im Lauf der nächsten 2—4 Tage stark hyperämisch. Das Anheilen des Transplantats verlief gut.

Die Ergebnisse dieser Versuche sind in einer Tabelle verzeichnet, in der auch Angaben gegeben sind über die Regeneration der Extremitäten im Stadium I bei einfacher Amputation im distalen Teil des Unterschenkels (Serie K), wie auch bei ihrer Amputation auf derselben Höhe bei gleichzeitiger autoplastischer Verpflanzung (Serie N).

Als volle Regeneration wurden die Fälle verzeichnet, in denen ein ganzer typischer 3—5-zehiger Fuss regenerierte; als teilweise Regeneration—die jenigen, in denen der regenerierte Fuss atypisch oder zweizehig war, und als gänzlich fehlende Regeneration die Fälle, in denen auf der Amputationswundfläche nur die Haut oder kleine unbestimmbare Auswüchse regenerierten.

Aus der Tabelle (S. 541) lässt sich folgendes schliessen.

Bei autoplastischer Verpflanzung des Mesoderms des Beines einer Kaulquappe im I Stadium verläuft die Regeneration nicht so gut, als bei autoplastischer Verpflanzung mit gleichzeitiger Amputation des ganzen Beines (Mesoderm und Epithel) im selben Stadium. Dieses wird bedingt durch die Schädigung des Mesoderms bei dessen Isolation vom Epithel, die im Stadium I schwer zu bemerkstelligen ist. Interessant ist es, dass die Bildung der teilweisen Regenerate sowohl in den vorliegenden, wie auch in meinen früheren Versuchen ([7]) jedesmal mit einer Abnahme der Quantität des aktiven Mesoderms auf der Amputationswundfläche verbunden war. Es ist anzunehmen, dass die Regeneration der Extremitäten bei den Kaulquappen mosaikartig und etwas anders vor sich geht, als bei den Urodelen.

Die Extremitäten regenerieren nicht in 1.5% der Fälle bei autoplastischer Verpflanzung des Mesoderms im Stadium I unter das Epithel (Serie Tsch); in 100%—bei Verpflanzung des Mesoderms im Stadium IIIa unter das Epithel von Kaulquappen Stadium I (Serie U); in 81.3%—bei autoplastischer Verpflanzung des Mesoderms im Stadium I unter verpflanztes Epithel Stadium IIIb—IV (Serie C); in 89.5%—bei Verpflanzung des Mesoderms im Stadium I unter das Epithel der Kaulquappen Stadium IIIa (Serie LIIIa); und in 69.0% der Versuche bei Verpflanzung des Mesoderms im Stadium I unter das Epithel der Kaulquappen Stadium IIb (Serie LIIb). Diese Ergebnisse lassen darauf schliessen, dass die Extremitäten ihre Regenerationsfähigkeit infolge der Veränderungen der Eigenschaften des Mesoderms und Epithels verlieren, wie auch infolge der Veränderung der Eigenschaften des humoralen Mittels ([1,2,8]). Die Veränderungen des Mesoderms im Stadium IIa sind reversibel und führen zur weiteren Entwicklung seiner histologischen Differenzierung; im Stadium IIb dagegen sind sie nicht reversibel und führen zur Veränderung der Eigenschaften seiner Zellen—zur histologischen Differenzierung.

Die Veränderungen im Epithel haben in den Stadien IIb, IIIa, IIIb, und IV einen progressiven Charakter und führen, augenscheinlich, zum Verlust seiner Fähigkeit mit dem Mesoderm in die Verbindung zu treten, die die Anhäufung der Mesodermalzellen in der Anlage bestimmt. Die die Regeneration hemmende Wirkung des humoralen Mittels zeigt sich deutlich im Stadium IIIa ([8]), tritt aber augenscheinlich schon im Stadium IIb ein ([1,2]). Die Rolle des Nervensystems beim Verlust der Regenerationsfähigkeit ist

Versuchsserie	Art der Operation	Zahl der Operationen	Misslungene Operationen	In frühen Stadien fixiert	Als Kontrolltiere zurückbehalten	Keine Regeneration		Teilweise Regeneration		Volle Regeneration	
						Zahl der Versuche	%	Zahl der Versuche	%	Zahl der Versuche	%
K	Amputation des Fusses im distalen Teil des Beines im Stadium I.	156	—	—	156	3	1.6	1	0.5	152	97.8
N	Autoplastische Verpflanzung des amputierten Beines im Stadium I	57	—	—	57	3	5.3	1	1.7	53	93.0
Tsch	Autoplastische Verpflanzung des Beinmesoderms im Stadium I unter das Epithel	68	—	—	67	1	1.5	12	17.9	54	80.6
U	Verpflanzung des Beinmesoderms im Stadium IIIa unter das Epithel einer Kaulquappe im Stadium I	48	—	3	45	45	100.0	—	—	—	—
L II b	Verpflanzung eines Beines im Stadium I unter das Epithel einer Kaulquappe im Stadium IIb	30	—	1	29	20	69.0	4	13.8	5	17.2
L III a	Verpflanzung des Mesoderms eines Beines im Stadium I unter das Epithel einer Kaulquappe im Stadium IIIa	21	—	2	19	17	89.5	—	—	2	10.5
C	Autoplastische Verpflanzung des Mesoderms eines Beines im Stadium I unter das verpflanzte Epithel im Stadium IIIb—IV	35	3	—	32	26	81.3	5	15.6	1	3.1

noch nicht festgestellt. Es ist nicht ausgeschlossen, dass die Extremitäten der Kaulquappen auch ohne Anteil des Nervensystems regenerieren können. Die Frage, ob die Eigenschaften des Epithels und Mesoderms sich beim Verlust der Regenerationsfähigkeit der Extremitäten unabhängig von den Veränderungen des humoralen Mittels verändern können, steht noch offen, und ich studiere sie weiter.

Aus den vorliegenden Ergebnissen müssen wir den Schluss ziehen, dass das Problem von der Wiederherstellung der Regenerationsfähigkeit der Extremitäten der Kaulquappen komplizierter wird, da der Verlust dieser Fähigkeit sowohl mit den Veränderungen des gesamten humoralen Mittels des Tieres zusammenhängt, wie auch mit den Veränderungen der Eigenschaften des Mesoderms und Epithels der Extremitäten.

Schlussfolgerungen. 1. Die Extremitäten der Kaulquappen verlieren während der Metamorphose ihre Regenerationsfähigkeit im Zusammenhang mit den progressierenden Veränderungen der Eigenschaften des Mesoderms und Epithels der Extremitäten.

2. Der Verlust der Regenerationsfähigkeit der Extremitäten hängt auch mit den Veränderungen des gesamten humoralen Mittels des Tieres zusammen ([1],[2],[3]). Die Rolle des Nervensystems in diesem Prozess ist noch nicht genügend erwiesen.

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EXPERIMENTELLE MORPHOLOGIE

ÜBER DIE BEDEUTUNG DES NERVENSYSTEMS BEI DER REGENERATION DER EXTREMITÄTEN BEI DEN ANUREN

Von L. W. POLEŽAJEW

(Vorgelegt von I. I. Schmalhausen, Mitglied der Akademie, d. 7. X. 1939)

Bei den Urodela ist für die Regeneration der formierten Extremitäten das Nervensystem notwendig ([11,12,13]). Denervierte Extremitäten können nicht regenerieren, sogar wenn die Denervierung nicht vor der Amputation des Organs, sondern nach derselben oder im Lauf seiner Regeneration ausgeführt wurde ([13]). Für die Regeneration ist offenbar das sympatische, und nicht das motorische oder sensorische Nervensystem notwendig ([12]).

Bei den Anlagen der Amphibien dagegen können die Extremitäten in der normalen Ontogenese sich ohne Beteiligung des Nervensystems entwickeln. Hinweise hierauf sind in der Literatur vorhanden ([2,3,1]), auch konnte ich selbst mich hiervon überzeugen, indem ich eine Entwicklung der Extremität bei Tritonanlagen bei der Explantation ihres Keimmaterials in eine Salzlösung ([6]) erhielt, wobei das Nervensystem, das Blutgefässsystem und andere Teile der Anlage im Explantat nicht enthalten waren.

Die Zellen der Anlage haben die Fähigkeit, die Extremität in der normalen Ontogenese unabhängig von dem Nervensystem zu bilden, die Zellen der formierten Extremität können, dagegen, bei ihrer Regeneration die Extremität ohne den stimulierenden Einfluss des Nervensystems auf dieselben nicht bilden. Folglich verändern sich die morphogenetischen Eigenschaften der Extremitätzellen im Laufe der Ontogenese ([7]). Offenbar treten diese Veränderungen nicht in der Anlage, sondern in der formierten Extremität ein. In diesem Fall kann man voraussetzen, dass in einem gewissen Stadium die bereits formierte Extremität zur Regeneration ohne Beteiligung des Nervensystems fähig ist. Mit dieser Voraussetzung stimmten folgende meine Beobachtungen gut überein: 1) Die transplantierten und gleichzeitig amputierten Extremitäten der Kaulquappen regenerieren sehr schnell, im Laufe von 8—12 Tagen, häufig ebenso schnell, wie die einfach amputierten Extremitäten. Hieraus ergibt sich die Wahrscheinlickeit, dass die Nerven keine Zeit haben, an das Transplantat heranzuwachsen, und dasselbe ohne Beteiligung des Nervensystems regeneriert, was mit Bestimmtheit von den ersten Regenerationsstadien gesagt werden kann. 2) Der auf den Schwanz der Kaulquappe transplantierte Stumpf der Extremität kann regenerieren, ungeachtet der Resorption des Schwanzes bei der Metamorphose, bei der das Nervensystem im Schwanz degeneriert. In diesem Fall mussten wenigstens die späten Regenerationsstadien ohne Beteiligung des Nervensystems verlaufen.

Diese Schlussfolgerungen und Beobachtungen veranlassten mich, die Frage über die Bedeutung des Nervensystems für die Regeneration der Extremitäten experimentell nachzuprüfen. Ausserdem untersuchte ich gleichzeitig die Frage über die Rolle des Nervensystems beim Verlust der Regenerationsfähigkeit der Extremitäten bei den Kaulquappen.

Als Versuchsobjekte wurden Kaulquappen der *Rana temporaria* im I Stadium ([8]) gewählt, wo das Gelenk zwischen dem Ober- und Unterschenkel noch nicht gegliedert ist, das Skelett verknorpelt ist, die Muskeln in aus Mesodermalzellen bestehenden Anlagen ([4],[5]) gebildet sind und wo bei der Amputation im distalen Teil des Unterschenkels die Beinchen fast in 100% der Fälle regenerieren ([8]). Der Versuch bestand darin, dass der rechte Hinterfuss zuerst im distalen Teil des Unterschenkels und dann am Rumpf amputiert wurde, wonach der aus Unter- und Oberschenkel bestehende Stumpf in eine im Bauchepithel gemachte Wunde autoplastisch verpflanzt wurde. Man konnte erwarten, dass das transplantierte Beinchen bei der Regeneration entweder die Nerven aus den umgebenden Geweben herabziehen und daher innerviert sein würde, oder dass die Regeneration ohne Beteiligung des Nervensystems erfolgen wurde. Zur Kontrolle wurde bei derselben Kaulquappe das linke Hinterbein im distalen Teil des Unterschenkels amputiert, in welchem bei der Regeneration der Verlauf der Nerven verfolgt werden musste. Als volle Regeneration wurde die Wiederherstellung eines typischen, fünfzehigen Beinchens betrachtet, als teilweise—die Wiederherstellung eines atypischen Beinchens oder eines Beinchens mit ungenügender Zehenzahl, als Fehlen der Regeneration—das Zuwachsen der Wundoberfläche mit Haut oder die Bildung kleiner unbestimmter Auswüchse.

I Serie. Der Versuch wurde im Sommer 1938 durchgeführt*. Der Stumpf des Beinchens wurde in das hintere Drittel der Bauchgegend transplantiert, welches nach den Angaben von Lebedinsky ([3]) am wenigsten innerviert ist. Das Epithel des Transplantats wuchs an das Epithel der Wundenränder des Bauches an, das Mesoderm des Transplantats lag am Bauchfell an. Von 150 Operationen wuchsen die Extremitäten in 83 Fällen an, von denen 3 Kaulquappen in frühen Regenerationsstadien fixiert wurden. Von den übrigen 80 Kaulquappen regenerierten die Versuchsbeinchen in 75 Fällen vollständig, in 3 Fällen teilweise und regenerierten nicht in 2 Fällen, während die Kontrollen in 73 Fällen vollständig, in 6 Fällen teilweise regenerierten und in 1 Falle keine Regeneration erfolgte. Somit verlief die Regeneration im Versuch und in der Kontrolle ganz gleich.

Nach Ablauf von 9—12 Tagen vom Moment der Amputation wurden nach vollständiger Regeneration der Extremitäten 32 Kaulquappen in Zenkerflüssigkeit für die nachherige histologische Bearbeitung nach Mallori und 51 Kaulquappen in Formalin für die nachherige Bearbeitung nach Belschowsky zwecks Auffindung der dünnen Nervenfasern fixiert. Leider gelang letzteres infolge eines technischen Missverständnisses nicht, so dass mir nur das nach Mallori gefärbte Material verblieb. Die Kaulquappen wurden so in Schnitte zerlegt, dass die Kontroll-Hinterbeine frontal zerschnitten wurden, die transplantierten dagegen in der Längsrichtung. In allen Fällen waren die Kontrollen stärker differenziert, als die transplantierten Beinchen. Bei den ersten begann das Skelett zu verknöchern, die Gelenke waren gegliedert, die Muskeln bestanden aus quergestreiften Fasern; bei den zweiten verknorpelte das Skelett blos, die Gelenke waren nicht gegliedert, die Muskeln bestanden nur aus Anlagen—dichten Anhäufungen in bestimmter Weise orientierter Mesodermalzellen. Die Differenzierung des Regenerats des Kontrollbeinchens unterschied sich sehr wesentlich von der Differenzierung der alten Gewebe des Organrestes und erinnerte sehr an die Differenzierung im Transplantat. In dem letzteren unterschieden sich die differenzierten mesodermalen Gewebe des Organrestes nur dadurch von den mesodermalen Geweben seines Regenerats, dass in denselben sich Stücke von Knochen oder altem Knorpel vorfanden—Teile, die sich nicht bis zum Schluss dedifferenziert hatten. Die gelblich-

* Diese Serie des Versuches wurde in meinen Auftrage von W. P. Krascheninnikowa ausgeführt.

grün gefärbten Nerven waren in dem Kontrollbeinchen gut sichtbar und auf den Serienschnitten liess sich ihr ganzer Verlauf von der Basis des Organrestes bis zum distalen Ende des Regenerats leicht verfolgen. Sie verliefen auf einem wesentlichen Teil des Weges neben den Blutgefässen zwischen den Muskeln und dem Skelett. In den verpflanzten Beinchen und deren Regeneraten wurden, trotz sorgfältiger histologischer Untersuchung der Präparate, Nerven nicht gefunden. Die Blutgefässe waren gut zu sehen, auch wurde ihr ganzer Verlauf, das Einwachsen in die Basis des Transplantats und die Verästelung in demselben, sowie in seinem Regenerat verfolgt.

Ich konnte jedoch die Daten vom Jahre 1938 nicht als endgültig betrachten, da die spezielle Bearbeitung des Materials mit Aufdeckung der Nervenfasern nach der Versilberungsmethode misslang. Daher führte ich 1939 eine zweite Versuchsserie durch.

II Serie. Die Methodik dieser Serie unterschied sich von unserer vorhergehenden Methode nur in zwei Punkten: 1) der Stumpf des Beinchens wurde nicht in das hintere Drittel, sondern in die Mitte des Bauches verpflanzt, die, meiner Ansicht nach, weniger innerviert ist, als das letzte Drittel; 2) zwecks besseren Anwachsens wurde vom proximalen Teil des Beinchens das Epithel entfernt, wonach das Beinchen unter das Epithel in ein im Bauch gemachtes Täschchen hineingeschoben wurde.

Von 65 Tieren kamen 2 um und in 6 Fällen fiel das Transplantat ab. Bei den übrigen 57 Kaulquappen regenerierten die Transplantate in 53 Fällen vollständig, in 2 Fällen teilweise und in 2 Fällen nicht; in der Kontrolle dagegen regenerierten sie in 54 Fällen vollständig, in einem Falle teilweise und in 2 Fällen nicht. Die Tiere wurden fixiert: 2 in einem Gemisch von 70° Alkohol mit Formalin zwecks totaler Erhaltung, 10 in Zenkerflüssigkeit zwecks Färbung nach Mallori und 45 in 96° Alkohol zur Versilberung der Nervenfasern nach Ramon-Kachal. Diesmal gelang die Versilberungsmethode gut. In dem Kontrollbeinchen und seinem Regenerat waren nicht nur die silbergeschwärzten dicken vielfaserigen Nervenäste, sondern auch die in einem dichten Netz die Gewebe durchziehenden feinsten Nervenfasern gut zu sehen. In dem verpflanzten Versuchsbeinchen konnte man nur die in Teile und Fasern zerfallenden, degenerierenden Nerven, die sich inmitten alter Gewebe befanden und zusammen mit diesen transplantiert worden waren, sehen; keinerlei andere Nerven konnten gefunden werden. Sie waren weder bei den in die Transplantatbasis hineinwachsenden Blutgefässen, noch in den Geweben des verpflanzten Beinchens, noch auch in seinem Regenerat vorhanden. In anderen Fällen begannen dünne Nervenfasern in die Transplantatbasis aus den umgebenden Geweben hineinzuwachsen.

Die Daten beider Serien des Versuches überzeugen uns davon, dass die in die Bauchgegend verpflanzten Extremitätenstümpfe der Kaulquappen ohne Beteiligung des Nervensystems regenerieren können und dass diese Regenerate sich morphologisch in keiner Hinsicht von den innervierten Regeneraten der Kontrollbeinchen unterscheiden. Somit bestätigen unsere Daten die von mir oben ausgesprochene Voraussetzung, dass die formierten Extremitäten bei den Kaulquappen ohne Beteiligung des Nervensystems regenerieren können, was wahrscheinlich davon abhängt, dass in diesem Stadium der Ontogenese in den Geweben der Extremitäten jene Veränderungen, die die Notwendigkeit des stimulierenden Einflüsses des Nervensystems für den Verlauf der Regeneration bedingen, noch nicht stattgefunden haben. Offenbar bezieht sich das auch auf die Regeneration des Schwanzes und anderer Organe. Verallgemeinernd kann man sagen, dass die Abhängigkeit der Regeneration von dem Nervensystem durch die ontogenetische Entwicklung des Organs bedingt ist und dass somit in einem gewissen Stadium das Organ auch ohne Beteiligung des Nervensystems regenerieren kann.

Kürzlich nachdem meine Arbeit im Wesentlichen bereits beendigt war, erschien der Artikel von Schaxel und Schneider ([10]), welche mitteilen, dass nach ihren Daten die Extremitäten bei grossen Axolotlen ohne Beteiligung des Nervensystems regenerieren können. Genaueres, insbesondere die Methodik der Aufdeckung des Nervensystems im Regenerat, teilen die Verfasser nicht mit. Daher ist es gegenwärtig schwer, die Divergenz zwischen ihren Schlussfolgerungen und den Schlüssen von Weiss ([13]) und Schotte ([11]), dass bei den Tritonen für die Regeneration der Extremitäten das Nervensystem notwendig sei, zu erklären.

Unsere Ergebnisse zeigen, dass im I Stadium die Extremitäten bei den Kaulquappen ebenso gut ohne Beteiligung des Nervensystems, wie unter Beteiligung desselben regenerieren können. Somit erfolgt der Verlust der Regenerationsfähigkeit im nächsten (II) Stadium nicht infolge von Veränderungen der Eigenschaften des Nervensystems, sondern infolge von Veränderungen der Eigenschaften anderer Gewebe der Extremität. Hiermit stimmen unsere Daten über die Veränderung der Eigenschaften des Mesoderms ([5],[6],[9]) und Epithels ([9]), im Zusammenhang mit denen die Regenerationsfähigkeit der Extremitäten bei den Anura verloren geht, gut überein. Es ist von Interesse eine Parallele zwischen den Anura und Urodela zu ziehen. Bei den Urodela führt die Veränderung der Eigenschaften der Extremitätengewebe nur zu einer Herabsetzung der Regenerationsfähigkeit der letzteren und zur Notwendigkeit für die Regeneration des stimulierenden Einflusses des Nervensystems. Bei den Anura, dagegen, ist die ontogenetische Veränderung der Eigenschaften der Extremitätengewebe so tiefgehend, dass die Extremitäten die Regenerationsfähigkeit sogar in Gegenwart des Nervensystems verlieren. Offenbar, steigern sich diese ontogenetischen Veränderungen der Gewebe, insbesondere des Mesoderms und Epithels, ebenso wie auch die Veränderungen in dem allgemeinen humoralen Mittel, im Zusammenhang mit der Erhöhung der philogenetischen Entwicklung der Tiere. Bekanntlich sind die Anura philogenetisch etwas höher entwickelt als die Urodela.

Die Frage über die Veränderung der Eigenschaften des Nervensystems in der Ontogenese in Bezug auf die Regenerationsfähigkeit der Organe erfordert eine weitere Bearbeitung.

Schlussfolgerungen: 1. Die in die Bauchgegend verpflanzten Extremitätenstümpfe (Ober- und Unterschenkel) können bei den Kaulquappen ohne Beteiligung des Nervensystems regenerieren.

2. Der Verlust der Regenerationsfähigkeit der Extremitäten bei den Kaulquappen ist nicht mit Veränderungen im Nervensystem, sondern mit Veränderungen der Eigenschaften in anderen Geweben der Extremität (in Mesoderm und Epithel) verknüpft.

3. Die Bedeutung des Nervensystems für die Regeneration ein und desselben, wenn auch schon formierten Organs ist in den verschiedenen Stadien seiner Ontogenese verschieden, da die Eigenschaften der Gewebe und Zellen des Organs sich in der Ontogenese verändern.

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EXPERIMENTELLE MORPHOLOGIE

ENTWICKLUNG DER MERKMALE DES DIMORPHISMUS BEI *DRYOBATES MAJOR* (L.)

Von B. G. NOWIKOW

(Vorgelegt von I. I. Schmalhausen, Mitglied der Akademie, d. 17. X. 1939)

Bei der Erforschung der Entwicklungsmechanik der Geschlechtsmerkmale der Vögel ([1],[5],[6] etc.) wurde festgestellt, dass die Pigmentierung des weiblichen Gefiedertypus bei Hühnern, Fasanen und Enten von dem Hormon des Eierstockes determiniert wird. Im Gegensatz dazu wurde später gezeigt ([3-4]), dass bei einigen Formen der Sperlingsvögel die Differenzierung einer Reihe von Merkmalen des beständigen Dimorphismus nicht von dem Hormon der Gonaden kontrolliert wird. Dieser Umstand veranlasste uns die Rolle der Geschlechtshormone bei der Entwicklung der sekundären Geschlechtsmerkmale an einigen Vertretern anderer Gattungen aufzuklären. Als geeignet und in dieser Beziehung bis jetzt noch unerforscht können die Spechtvögel (*Picariae*) angesehen werden. Auf Grund der Beobachtungen von Heinroth ([2]) in einem Fall lateraler Gynandromorphismus an dem Gefieder des amerikanischen Spechtes (*Calaptus auratus*) kann man annehmen, dass die Entwicklung der Merkmale des Dimorphismus am Gefieder der Spechtvögel, wie auch bei einigen Arten der Sperlingsvögel, durch die Eigenschaften des federbildenden Gewebes selbst bestimmt wird. In der vorliegenden Arbeit bringen wir die Resultate der Experimente, welche die Frage über die Bedeutung der Geschlechtshormone bei der Ausbildung der Merkmale des Dimorphismus im Gefieder des grossen Buntspechts (*Dryobates major*) aufklären sollen. Das Juvenalgefiederkleid bei dieser Art zeigt keinen Geschlechtsdimorphismus, und unterscheidet sich von dem Federkleider der erwachsenen Vögel durch eine hell rote Färbung der Federn am Oberkopf. Bei den erwachsenen Männchen sind die Federn am Oberkopf schwarz, und haben am Nacken einen roten Querstreifen. Den erwachsenen Weibchen fehlt die rote Pigmentierung der Federn des Kopfes vollständig. Ausser der Gefiederfärbung besteht noch ein Unterschied zwischen den Geschlechtern der erwachsenen Vögeln in der Struktur der Federn genannter Pterylien. Die Federn des Nackens haben in der Konturzone massive Strahlen erster Ordnung, welche diffus Zooneretrin enthalten und keine Strahlen zweiter Ordnung besitzen (Abb. 1, *b* und *c*). Merkwürdig ist dass die roten Federn des Oberkopfes der jungen Vögel dieselbe Struktur haben (Abb. 1, *a*). Der beschriebene Unterschied in Färbung und Struktur der Kopffedern ist bei dem grossen Buntspecht ein ständiges sekundäres Geschlechtsmerkmal.

Der Einfluss der Gonaden auf die Entwicklung dieser Merkmale wurde durch Kastration und Injektion von Geschlechtshormonen geklärt. Die Unter-

suchung wurde an 8 jungen und 4 alten Vögeln ausgeführt. Die jungen Vögel wurden ungefähr im Alter von 1 Monat operiert, jedenfalls lange Zeit vor dem Eintritt der Juvenalmauser. Nach Beendung der Beobachtungen wurde die Reinheit der Operation in allen Fällen mikroskopisch nachgeprüft. Die Färbung und Struktur wurden an den neuen Federgenerationen der dimorphen Pterylien, welche sich nach der natürlichen Mauser, so wie nach dem Rupfen entwickelten, ebenfalls untersucht.

Versuche mittels Ovariotomie. Die weibliche Geschlechtsdrüse wurde bei 3 jungen und 1 alten Specht entfernt; zwei normale Weibchen dienten als Kontrolle. Volle Ovariotomie wurde in drei Fällen erreicht. Die Entwicklung einer Gonade auf der rechten Seite konnte in keinem Falle beobachtet werden. Die Juvenalmauser der operierten und Kontrollvögel begann Mitte August. Zu Beginn Novembers waren die Juvenalfedern des Kopfes vollständig durch definitive Federn ersetzt. Bei allen ovariotomierten Vögeln entwickelten sich nach der Mauser Federn, die der

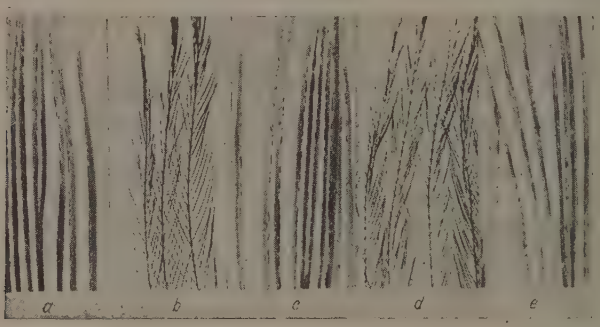

Abb. 1. Mikrophoto der Federn der normalen und kastrierten Vögel (× 37): *a*—juvenale Feder, *b*—Feder des normalen Weibchens, *c*—Feder des normalen Männchens, *d*—Feder des kastrierten Weibchens, *e*—Feder des kastrierten Männchens.

Farbe und Struktur nach typisch für normale Weibchen sind. Die Strahlen erster Ordnung der Konturzone der Federn des Nackens waren wie bei ovariotomierten, so auch bei Kontrollvögeln nicht massiv, sondern fein und besassen gut entwickelte Strahlen zweiter Ordnung (Abb. 1, *d*). Das rote Pigment fehlte. Die neue Federgeneration, nach künstlicher Entfernung der alten Federn, zeigte bei jungen, wie bei alten Vögeln in allen Fällen dasselbe Resultat.

Versuche der Kastration der Männchen. Diese Serie bestand aus 4 operierten und 3 Kontrollvögeln. Nach Abschluss der Beobachtung konnte die volle Entfernung der männlichen Drüsen in allen Fällen konstatiert werden. Die makro- und mikroskopische Untersuchung der regenerierten Federn und der neuen Federn nach der natürlichen Mauser zeigten, dass die Entfernung der männlichen Geschlechtsdrüsen keinen Einfluss auf die Entwicklung der männlichen Merkmale hat. An allen operierten Vögeln entwickelte sich der rote Querstreifen auf dem Nacken, ebenso wie bei den Kontrollvögeln. Den Strahlen erster Ordnung dieser Federn fehlen, so wie bei der Norm, die Strahlen zweiter Ordnung; sie enthalten diffuses rotes Pigment (Abb. 1, *e*).

Versuche mit Injektion von Geschlechtshormonen. In dieser Serie wurden 3 kastrierten Männchen täglich 50 oder 100 ME Follikulin injeziert. Die Injektion wurde einen Tag nach der Rup-

fung begonnen und bis zur vollen Ausbildung neuer Federn ausgeführt. Die Injektion von Follikulin unabhängig von der Dose hatte keinen Einfluss auf die Entwicklung der Färbung und Struktur der Federn des Nackens: die Strahlen zweiter Ordnung fehlten in der Konturzone dieser Federn, und die Strahlen erster Ordnung waren intensiv rot gefärbt.

Die ausgeführte Beobachtungen zeigen zusammenfassend, dass die Entwicklung der Merkmale des Geschlechtsdimorphismus am Gefieder des grossen Buntspechts nicht von den Geschlechtshormonen kontrolliert wird.

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EXPERIMENTELLE MORPHOLOGIE

EINFLUSS DER GONADEN AUF DIE ENTWICKLUNG DER GESCHLECHTSMERKMALE BEI *FRINGILLA MONTIFRINGILLA* (L.)

Von B. G. NOWIKOW

(Vorgelegt von I. I. Schmalhausen, Mitglied der Akademie, d. 17. X. 1939)

In unseren früheren Untersuchungen wurde gezeigt ([1–3]), dass im Gegensatz zu den Merkmalen des beständigen Dimorphismus, die Entwicklung der Merkmale des Saisondimorphismus bei einigen Arten der Sperlingsvögel (*Fringilla coelebs*, *Passer domesticus*) von den Hormonen der Geschlechtsdrüsen bestimmt wird. Ein solches Merkmal des Saisondimorphismus, wie die periodische Umfärbung des Männchenschnabels des Buchfinks, steht in kausaler Beziehung mit der hormonalen Aktivität der männlichen Geschlechtsdrüsen. Nach Entfernung der Gonaden behält das Männchen permanent die Hornfarbe des Schnabels bei. Bei der Injektion männlichen Geschlechtshormons entwickelt sich die Hochzeitsfarbe bei beiden Geschlechtern.

Es ist bekannt, dass bei einigen dem Buchfink nahestehenden Formen die Saisonumfärbung des Schnabels in gleichem Masse bei beiden Geschlechtern stattfindet. So kann zum Beispiel beim Bergfink (*Fringilla montifringilla*) während der Periode der Geschlechtsaktivität die Entwicklung der blau-schwarzen Hochzeitsfarbe des Schnabels bei beiden Geschlechtern beobachtet werden. Nach Champy gehört dieser Fall zu den sogenannten ambosexuellen Merkmalen. Es entsteht hier die Frage über den Mechanismus der Entwicklung solcher Hochzeitsmerkmale, welche sich gleich bei beiden Geschlechtern äussern. Man kann annehmen, dass die Entwicklung der ambosexuellen Merkmale bei dem Weibchen durch das Ovarialhormon und bei dem Männchen durch das Testikelhormon induziert wird. Es ist aber auch nicht ausgeschlossen, dass dieses Merkmal bei beiden Geschlechtern von einem Hormon bestimmt wird. Ausgehend von den Tatsachen, dass bei *Fringilla coelebs* die Entwicklung des Hochzeitsmerkmals beim Männchen vom Testikelhormon abhängt, und der Möglichkeit der Induktion dieses Merkmals beim Weibchen durch dasselbe (Testikel) Hormon, müssen wir annehmen, dass bei *Fringilla montifringilla* die Saisonumfärbung des Schnabels bei beiden Geschlechtern durch das männliche Geschlechtshormon induziert wird, welches beim Weibchen durch die meduläre Zone des Eierstockes produziert wird. Zwecks Lösung der Frage über die Faktoren, welche die Entwicklung der ambosexuellen Merkmale kontrollieren, haben wir Versuche an Bergfinken (*Fringilla montifringilla*) ausgeführt. Gleichzeitig mit den Untersuchungen der ambosexuellen Merkmale, wurde auch die Rolle der Geschlechtshormone in der Differenzierung der Merkmale des beständigen Dimorphismus in der Gefiederfärbung erforscht. Zu den ambosexuellen Merkmalen beim Bergfinken gehört die periodisch wechselnde Färbung des Schnabels. Während der Periode der Geschlechtsruhe ist der Schnabel bei Männchen und Weibchen horn-gelb gefärbt (Abb. 1, *b*, *d*). Mit dem Eintritt der Geschlechtsaktivität, wird bei beiden Geschlechtern eine Umfärbung des Schnabels in blau-schwarz beobachtet (Abb. 1, *a*, *c*).

Die beständigen Geschlechtsunterschiede dieser Art äussern sich in der Gefiederfärbung. Beim Männchen sind die Federn des Kopfes, des Rückens, die Deckfedern des Flügels glänzend schwarz; Kehle, Kropf, untere Seite der Brust und Schulterfedern gelb-rötlich gefärbt. Die Weibchen sind bleicher gefärbt; die glänzend schwarze Farbe ist bei ihnen durch dunkelbraune Farbe ersetzt, die gelb rote Farbe ist weniger ausgebildet, als bei den Männchen.

Die Untersuchungen über die Rolle der Gonaden bei der Entwicklung der Geschlechtsmerkmale wurden 1937—1938 nach folgendem Plan ausgeführt: 1) Gonadektomie, 2) Transplantation der Gonaden, 3) Injektion von Geschlechtshormonen.

Versuche mittels Gonadektomie. Diese Serie bestand aus 65 Versuchs- und Kontrollvögeln. Die Gonaden wurden im Herbst und Winter entfernt. Zur Zeit der Operation waren die Schnäbel aller Vögel horngelb gefärbt (Winterfarbe). Vollständige Kastration wurde bei 15 Weibchen und 26 Männchen erreicht. Die Beobachtungen an den Versuchs- und Kontrollvögeln wurden während des ganzen Jahres ausgeführt. Als Resultat dieser Beobachtungen wurde festgestellt, dass bei rein kastrierten Vögeln die Saisonumfärbung des Schnabels ausbleibt. Die Winter-horn-gelbe Farbe des Schnabels der operierten Männchen und Weibchen zeigte während des ganzen Jahres keine Veränderungen. Bei den Kontrollvögeln konnte eine normale Umfärbung des Schnabels beobachtet werden. Jedoch auf die Entwicklung der Merkmale des beständigen Dimorphismus hatte die Kastration keinen Einfluss. Die neue Federgeneration der ovariotomierten Vögel zeigte in der Färbung keine Abweichung von der Norm. Analoge Resultate wurden auch an kastrierten Männchen erhalten. Unabhängig von der Operation entwickelte sich bei allen Vögeln dieser Serie nach der natürlichen Mauser normales Gefieder mit männlicher Färbung.

Abb. 1. Die Veränderungen der Pigmentation des Schnabels beim Bergfinken. *a*—Hochzeitsfarbe eines Weibchenschnabels; *b*—Winterfarbe eines Weibchenschnabels; *c*—Hochzeitsfarbe eines Männchenschnabels; *d*—Winterfarbe eines Männchenschnabels; *e*—Hochzeitsfarbe des Schnabels eines kastrierten Männchens, welche sich nach der Injektion von Androsteron entwickelte; *f*—Hochzeitsfarbe des Schnabels eines kastrierten Weibchens nach der Injektion von Androsteron.

Die angeführten Beobachtungen zeigen folglich, dass die Differenzierung der Merkmale des beständigen Geschlechtsdimorphismus in der Gefiederfärbung bei *Fringilla montifringilla* nicht von den Geschlechtshormonen abhängt. Die Entwicklung der ambosexuellen Merkmale steht umgekehrt unter der Kontrolle der Gonaden. Durch die Kastrationsversuche wurde festgestellt, dass die Entwicklung der ambosexuellen Merkmale von den Gonaden abhängt; diese Versuche lösen aber die Frage nicht, durch welches Hormon beim Männchen und Weibchen dies Merkmal realisiert wird. Antwort auf diese Frage geben die Versuche mit Gonadentransplantation und die Injektion der Geschlechtshormone.

Versuche mittels Gonadentransplantation. Versuche mit Kreuztransplantationen der Gonaden wurden an 4 Männchen und 4 Weibchen im Herbst 1938 veranstaltet. Sofort nach der Entfernung des Eierstockes wurde in die Leibeshöhle der Weibchen männliche Geschlechtsdrüsen transplantiert. Die Transplantation der Eierstöcke in Männchen wurde analog ausgeführt. Nach der Operation wurden alle Versuchs- und Kontrollvögel in ein spezielles Zimmer gebracht und bekamen täglich 14 Stunden lang künstliches Licht. Anfangs November entwickelte sich infolge dieser Beleuchtung bei allen Kontrollvögeln am Schnabel die blau-schwarze Hochzeitsfarbe. Von den 8 operierten Vögeln entwickelte sich dieses Merkmal nur bei 2 Weibchen. Die Sektion dieser Vögel zeigte, dass die überpflanzten Testikel an der Stelle des entfernten Eierstockes eingeheilt waren und dieselbe Grösse hatten, wie die Testikel der normalen Männchen während der Hochzeitsperiode. Die Eileiter dieser Vögel waren reduziert und Reste des Eierstockes waren nicht vorhanden. Bei den anderen Vögeln waren die transplantierten Gonaden vollständig resorbiert, und die Schnäbel behielten die Winterfarbe. -

Versuche mittels Injektion von Geschlechtshormonen. Die Versuche mit Injektion von Geschlechtshormonen wurden an 46 normalen und kastrierten Vögel beiderlei Geschlechts ausgeführt. Einem Teil der Vögel wurde Follikulin (Kristalle gelöst in Öl), dem anderen Teil—Androsteron injeziert. In der Tabelle sind die Resultate wiedergegeben.

Der positive Effekt der Injektion ist mit dem +Zeichen, der negative Effekt mit dem—Zeichen gegeben. Aus den in der Tabelle angeführten Angaben ist zu ersehen, dass unabhängig von der Menge des injezierten Follikulins das Resultat auf die Pigmentation des Schnabels negativ war (Serie 1—6). Die Schnäbel der Männchen und Weibchen, welche der Einwirkung von Follikulin unterworfen wurden, änderten ihre Winter-horn-gelbe Farbe nicht. Nur der Eileiter reagierte auf das Follikulin. Unter Einwirkung der Injektion

Art der Vögel	Nr. der Serie	Geschlecht	Zahl der Vögel	Art des Hormons	Dose in γ	Dauer der Einwirkung in Tagen	Effekt an der Pigmentation des Schnabels	Effekt am Eileiter
Fringilla montifringilla	1	Weibchen	3	Follikulin	2	20	—	+
	2	»	3	»	4	20	—	+
	3	»	3	»	6	20	—	+
	4	Männchen	4	»	2	20	—	—
	5	»	4	»	4	20	—	—
	6	»	5	»	6	20	—	—
	7	»	3	Kontrolle	—	—	—	—
	8	Weibchen	4	»	—	—	—	—
	9	»	2	Androsteron	25	20	+—	—
	10	»	2	»	100	20	+	—
	11	Männchen	3	»	25	20	+—	—
	12	»	3	»	50	20	+	—
	13	»	2	»	100	20	+	—
coelebs	14	Männchen	1	Androsteron	25	20	—	—
	15	»	2	»	50	20	—	—
	16	»	2	»	100	20	+	—
	17	Weibchen	1	»	50	20	—	—
	18	»	2	»	100	20	+—	—

des weiblichen Geschlechtshormons wurde bei allen Vögeln starke Hypertrophie des Eileiters beobachtet.

Ganz andere Resultate wurden als Folge der Injektion von männlichem Geschlechtshormon erhalten (Serie 9—12). Schon am 6—7 Tage nach dem Beginn der Injektion von Androsteron wurde die winter-gelbe Farbe des Schnabels der Männchen und Weibchen allmählich durch die blau-schwarze Hochzeitsfarbe ersetzt (Abb. 1, *e*, *f*). Die Folgerichtigkeit der Umfärbung der einzelnen Stellen des Schnabels ging analog dem normalen Prozess vor sich. Zum 12 Versuchstage hatten schon alle Vögel die typische Hochzeitsfarbe. Die Dose von 25 γ war weniger effektiv. Die Pigmentation des Schnabels der Vögel dieser Serie war weniger vollständig, als in den anderen Fällen. Die Injektion eines Teiles dieser Vögel zeigte, dass das Androsteron keinen Einfluss auf die Entwicklung des Eileiters hatte.

Zusammenfassend zeigen die angeführten Angaben, dass die Entwicklung der ambosexuellen Merkmale bei *Fringilla montifringilla* durch das männliche Geschlechtshormon induziert wird. Das Follikulinhormon bestimmt die Hypertrophie des Eileiters, hat aber keinen Einfluss auf die Saisonumfärbung des Schnabels bei dem Weibchen. Wir können zugeben, dass bei normalen Verhältnissen die Hochzeitsfarbe des Schnabels bei Weibchen durch männliches Geschlechtshormon induziert wird, welches die meduläre Zone des Eierstockes produziert. Wenn das männliche Geschlechtshormon bei dem Weibchen nur in der medulären Zone gebildet wird, so muss man voraussetzen, dass die hormonale Aktivität dieses Teiles des Eierstockes ebenfalls jahreszeitlichen Veränderungen unterworfen ist.

Die Resultate der ausgeführten Versuche zeigen, dass zwichen dem Mechanismus der Realisation der ambosexuellen Merkmale und den Merkmalen des Saisondimorphismus Ähnlichkeit besteht. Die Ähnlichkeit äussert sich vor allem darin, dass beide Erscheinungen durch das männliche Geschlechtshormon bestimmt werden.

Im Zusammenhang damit entsteht jetzt die Frage, wie es kommt, dass bei Arten, wo ein Saisondimorphismus vorhanden ist, sich das Hochzeitsmerkmal nur bei Männchen entwickelt. Man kann annehmen, dass die Gewebe dieser Arten schwerer auf das Hormon reagieren. Am Schluss der Tabelle werden die Resultate der Injektion von männlichem Geshlechtshormon an Buchfinken angeführt, welche einen Vergleich der Empfindlichkeit der Gewebe, die die ambosexuellen Merkmale und die den Saisondimorphismus bilden, zulassen. Bei *Fringilla coelebs*, wie schon oben bemerkt, entwickelt sich die Hochzeitsfarbe des Schnabels nur bei dem Männchen, und wird von den Gonaden kontrolliert. Aus den Angaben (Serie 14—18) folgt, dass die Gewebe des Schnabels des Buchfinks weniger empfindlich gegen das Hormon sind, als die Gewebe des Schnabels bei dem Bergfink, wo sich ambosexuelle Merkmale ausbilden. Wenn bei den Bergfinken ein positives Effekt schon mit 25 γ Androsteron erreicht wird, so wird dasselbe Resultat beim Buchfink erst mit 100 γ erreicht. Die Weibchen des Buchfinken, wie schon früher von uns festgestellt, reagieren schwerer auf das Hormon als die Männchen. Diese Gegenüberstellung zeigt eine verschiedene Empfindlichkeit gegen das Geschlechtshormon der Schnabelgewebe zwischen *Fringilla coelebs* und *Fringilla montifringilla*. Hieraus folgt der Schluss, dass eine der Bedingungen der Äusserung der ambosexuellen Merkmale bei *Fringilla montifringilla* die Erhöhung der Empfindlickeit der Gewebe in der Reaktion auf das männliche Geschlechtshormon ist.

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EXPERIMENTELLE MORPHOLOGIE

ANALYSE DES MECHANISMUS DER SAISONVERÄNDERUNGEN AM FEDERKLEID BEI *LAGOPUS LAGOPUS* (L.)

Von B. G. NOWIKOW

(Vorgelegt von I. I. Schmalhausen, Mitglied der Akademie. d. 17. X. 1939)

Die weissen Rebhühner unterscheiden sich durch ihre jahrzeitlichen Veränderungen in der Gefiederfärbung sehr stark von den anderen Formen. Spezielle Untersuchungen der Ornithologen ([1] und and.) haben gezeigt, dass das Männchen und Weibchen der weissen Rebhühner im Laufe des Jahres mehrere Saisontypen der Befiederung haben. Johnsen konnte für das Männchen 4 Federkleider feststellen: ein Winter-, Frühlings-, Sommer- und Herbstkleid. Bei dem Weibchen fehlt das Frühlingskleid, und das Winter-, Sommer- und Herbstkleid unterscheiden sich durch eine schwache Farbänderung. Die Winterfedern, die bei beiden Geschlechter gleich sind, sind durch weisse Farbe, durch starke Entwicklung des Dünenteils der Federn und den s. g. Afterschaft charakterisiert. Die Frühlingsfedern der Männchen, welche eine kastanienbraune Färbung haben, entwickeln sich zuerst am Kopf, Hals, Kropf und nach 15—20 Tage auch auf den anderen Teilen des Körpers (Rücken, obere Seite des Flügels u. s. w.). Das Frühlingskleid wird schon nach kurzer Zeit durch das Sommerkleid erserzt. Letzteres unterscheidet sich von Frühlingskleid durch bleiche rot-braune Färbung und schwarzen Querstreifen auf der Federfahne. Während der nachfolgenden Mauser wird das Sommerkleid des Männchens durch das Herbstkleid ersetzt, welches sich durch mehr dunkel-braun-rote Federfärbung auszeichnet. Nach der Bildung des Herbstkleids beginnt die Formierung des weissen Winterkleids, wo schon keine rot-braunen und schwarzen Pigmente mehr vorhanden sind. Diese Federn entwickeln sich zuerst an der unteren Seite des Rumpfes, an den anderen Körperteilen etwas später. Bei den Weibchen zum Unterschied von den Männchen geht die Frühlingsmauser gleichzeitig an allen Pterylien vor sich. Das sich entwickelnde Sommerkleid ist weniger intensiv gefärbt, als bei den Männchen; diese Federn sind ockergelb mit breiten schwarzen Streifen und Flecken. Die Federn der oberen Seite sind dunkel mit bleich gelben Streifen und Flecken. Das Sommerkleid des Weibchens ähnelt etwas dem Juvenalkleid. Das Herbstkleid des Weibchens steht dem entsprechenden Kleid des Männchens nahe und charakterisiert sich durch einen starken Stich ins braune. Es muss betont werden dass bei beiden Geschlechtern, ausser denen hier genannten Federtypen, auch Federn mit Übergangsfärbung vorkommen. Die grossen Federn des Schwanzes und die unteren Deckfedern des Flügels wechseln nur einmal während des Jahres und halten ein und dieselbe Farbe bei.

Der jahreszeitliche Wechsel von Federn und Farbe bei den weissen Rebhühnern ist ein sehr komplizierter Prozess und zweifellos ein adaptives Merkmal, welches eine Anpassung an die Umgebung ist und eine wichtige Rolle in der Biologie der Fortpflanzung spielt. Mit unserer Arbeit versuchten wir die Natur der Faktoren zu ermitteln, welche die Realisierung dieses Merkmales in der Ontogenese bestimmen. Es schien wahrscheinlich, dass die Entstehung dieser Anpassungsfärbung während des Evolutionsprozesses auf einer morphogenetischen Korrelation mit dem endokrinen System beruht. Davon ausgehend, dass dieses Merkmal einen Saisoncharakter trägt, haben wir angenommen, dass es von solchen endokrinen Drüsen kontrolliert werden kann, deren hormonale Aktivität ebenfalls jahreszeitlichen Schwankungen unterworfen ist. Da der Anfang der Umfärbung des Gefieders mit der Periode der Geschlechtsaktivität chronologisch zusammenfällt, war es auch ganz natürlich, dass wir unsere Untersuchungen mit der Klärung der Rolle der Geschlechtsdrüsen begannen.

In letzter Zeit wurde festgestellt ([2,3]), dass die Entwicklung der sogenannten ambosexuellen Merkmale bei den Vögeln von dem Geschlechtshormon bei beiden Geschlechtern induziert wird (durch das Männliche). Uns schien wahrscheinlich, dass bei den weissen Rebhühnern die Bildung der pigmentierten Federn bei beiden Geschlechtern durch das Geschlechtshormon kontrolliert wird, und die Modifikation des Bildes nach Jahreszeit und Geschlechts mit den Schwankungen der Quantität des Hormons während der Federbildung in Verbindung steht. Die Resultate unserer Beobachtungen über den Einfluss der Geschlechtsdrüse auf die Saisonfärbung des Gefieders des weissen Rebhuhns (*Lagopus lagopus* L.) werden in dieser Mitteilung gebracht. Die Versuche bestanden einerseits in der Bestimmung der Zeit der Determination der Flühlingsfarbe der Federn und andererseits in der Bestimmung der Folge der Kastration. Unsere Angaben beziehen sich hauptsächlich auf die Frage über die Faktoren, welche sich auf die Entwicklung des Frühlings- und Sommerkleids beziehen. Die Experimente wurden 1938 und 1939 an 15 Weibchen und 30 Männchen ausgeführt.

Zeit der Determination der Frühlingsfärbung. Zwecks Feststellung der Determinationszeit der Frühlingsfedern wurden periodisch die Federn an normalen Vögeln gerupft. Angefangen im Januar, wurde alle 10 Tage bei den Männchen und Weibchen eine kleine Anzahl Federn an verschiedenen Körperteilen ausgerupft. Als Resultat wurde festgestellt, dass die Federpapillen lange Zeit vor dem Eintritt der Frühlingsmauser, schon die Fähigkeit haben Pigment zu bilden. Nach den Rupfungen mitte Januar regenerierten schon Federn mit Mosaikfärbung. Dieser Effekt konnte aber bei den Männchen nicht an allen Pterylien gleichzeitig beobachtet werden. Die Potenz zur Entwicklung der rot-braunen Farbe entsteht am Kopf und oberen Teil des Halses und nur nach einiger Zeit auf den anderen Pterylien (unterer Hals, obere Seite des Körpers, Deckfedern des Flügels, Seite und Kropf). Bedeutend später bekommen die Papillen der unteren Seite des Körpers diese Eigenschaft. Im allgemeinen muss gesagt werden, dass die Determination der Frühlingsfärbung der Federn auf den einzelnen Pterylien des Männchens mit derselben Folgerichtigkeit vor sich geht, wie die Frühlingsmauser. Bei den Weibchen entsteht die Fähigkeit zur Pigmentablagerung zu derselben Zeit, wie bei den Männchen, nur ist die Zeit zwischen den einzelnen Pterylien geringer. Ausserdem wurde festgestellt, dass bei den Weibchen Ende Januar und Anfangs Februar die regenerierten Federn keine typische Sommerfarbe hatten; diese hatten eine gelbe Farbe und fast ohne schwarzes Pigment. Die parallelen Untersuchungen der Gonadenaktivität zeigten, dass die Papillen die Fähigkeit zur Pigmententwicklung noch zu solcher Zeit haben, welche als Periode der Geschlechtsruhe

charakterisiert werden kann. So, im Januar und Februar, wo schon Federn mit pigmentierten Rändern regenerieren, befinden sich die Gonaden und Leitgänge noch im Depressionszustand. In den Testikeln konnten nur Spermatogonien beobachtet werden. Schon auf Grund dieser Angaben kann man annehmen, dass die Geschlechtsdrüse kein Faktor ist, welcher die Umfärbung des weissen Rebhuhns kontrolliert. Endgültig wurde diese Frage durch die Kastrationsversuche gelöst.

Kastrationsversuche. Zur Beobachtung hatten wir 15 kastrierte Männchen und Weibchen zur Verfügung. Die Operation wurde im Januar und in der ersten Hälfte Februar ausgeführt. Bei einem Teil der Vögel hatten die Federpapillen zur Zeit der Operation noch nicht die Potenz zur Entwicklung der Frühlingsfärbung. Mitte März begann bei allen Vögeln die natürliche Mauser, welche normal verlief. Bei allen Männchen, ganz unabhängig von der Zeit der Kastration, entwickelte sich nach der Mauser ein typisches Frühlingskleid (Abb. 1), welches später durch das Sommerkleid ersetzt wurde. Die Resultate an den kastrierten Weibchen waren dieselben; bei allen ovariotomierten Vögeln entwickelte sich nach der Frühlingsmauser ein normales Sommergefieder. Ein kastriertes Männchen wurde 15 Monate beobachtet, und immer zu bestimmter Zeit entwickelte sich ein Frühlings-, Sommer-, Herbst- und Winterkleid.

Abb. 1. Kastriertes Männchen.

Abb. 2. Normales Männchen.

Somit zeigen die Kastrationsversuche, dass die Saisonumfärbung des Gefieders bei weissen Rebhühnern nicht von den Geshlechtshormonen abhängt. Aber ein solches Merkmal des Saisondimorphismus, wie die Vergrösserung während der Fortpflanzungsperiode der s. g. «Augenbrauen», steht in Abhängigkeit von der Geschlechtsaktivität. Während der Periode der Geschlechtsruhe stellen diese «Augenbrauen» ein doppelt zusammengelegtes Hautläppchen mit bleich-roter Färbung dar. Bei dem Männchen beginnen sie im Frühling zu wachsen, strecken sich und erhalten eine hell-rote Färbung. Bei den Weibchen sind Saisonveränderungen nach Grösse und Färbung diese Gebilde bedeutend weniger vorhanden. Bei den kastrierten Vögeln bleiben diese «Augenbrauen» beständig unentwickelt. Auf Grund der erhaltenen Resultate können wir schliessen, dass die jahreszeitliche Veränderung der Gefiederfarbe bei weissen Rebhühnern nicht von den Geschlechtsdrüsen abhängt. Diese bestimmen aber die Saisonhypertrophie der «Augenbrauen» bei beiden Geschlechtern.

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EXPERIMENTAL MORPHOLOGY

PRE-NATAL DEVELOPMENT OF THE COAT OF SOME FINE-WOOLED BREEDS OF SHEEP

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The present investigation of the development of the coat in foetuses of the Merino Askania Rambouillet and the mouflon Precoce is the second stage in the study of the fleece embryogenesis. The first investigation of this kind was carried out on the Kirghiz «kurdyuk» (fat-rumped, *Steatopygae*) sheep (Terentieva, 1935), as a coarse-wooled breed; the second—on the Merino Askania Rambouillet and Precoce as a fine-wooled breed. The object of the present work is to study the formation of hairs in the sheep embryo, which will make it possible to reveal the peculiarities in the development of the coat of fine-wooled sheep. We might as well say that the process of the fleece development in the embryogenesis has not received sufficient attention in literature. This deficiency has been pointed out by M. F. Ivanov (1), Nikolskaya (1932), Galpin (3) and others.

The study of the fleece development was carried out on foetuses of the Merino Askania Rambouillet (100 specimens) and Precoce (36 specimens). Foetuses at the age of 38 to 150 days were grouped according to the stage of development. Each stage included embryos of definite ages, for instance: 1st stage—38—43 days, 2nd stage—45—48 days, etc.

The process of hair formation in the Merino and Precoce begins in 38—40—42-day foetuses. In that stage occurs the formation of sensory follicles which develop originally in the region of the supraorbital arches. At this stage of development they have a rounded shape and an appreciably darker colour than the skin. They measure 60 μ in diameter. In foetuses of this age the epidermis is uniformly thick all over the body, equalling 15 μ, whereas the thickness of the corium varies, e. g. on the forehead it measures 50 μ, on the poll 45 μ, on the belly 100 μ. At the age of 47—53 days in the coronary region of foetuses occurs the initial formation of rudiments of coarse hairs. In some cases this process begins at 47—48 days of pre-natal life, in others at 50—51 days. In 53-day foetuses rudiments of coarse (kemp) hairs are plainly visible even under a magnifying glass. No hair rudiments of coarse hair have been found to appear at earlier stages.

At the same age occurs the development of coarse hairs in foetuses of the Kirghiz «kurdyuk» sheep (2). The same condition is described by Galpin in foetuses of the Romney-Marsh breed. Consequently, the process of initial formation of coarse hair rudiments in fine- and coarse-wooled breeds occurs simultaneously, approximately within the period of 47—53 days of pre-natal development. It should be noted that in embryos at this age the thi-

ckness of the corium increases but on the forehead where it attains 120 μ, and it is exactly here that at the given time the development of the coarse-fibre follicles take place.

The process of formation of hair follicles seems to be connected with the presence of a corium of definite thickness. Thus for instance, in 58-day foetuses coarse-fibre follicles have already covered the head and the adjoining part of the neck where the corium attained 120 μ in thickness.

A second instance: in 61-day foetuses the thickness of the corium on the head is 125 μ, and it is here that the development of coarse-hair follicles is observed; on the neck the thickness of the corium is less than 115 μ, and no development of hair rudiments is to be found. And only at the age of 62—63 days all the foetuses have the head and part of the neck adjoining the head covered with coarse-hair follicles, for this is the time when the thickness of the corium exceeds 120 μ. It should be noted that during the period of the prenatal development, on the 58—63 day occurs an intensive thickening of the corium over the entire body. Its thickness on the forehead in a 63-day foetus attains 200 μ, on the back 150 μ, on the side 180 μ, on the thigh 150 μ, on the belly 180 μ. The thickness of the epidermis remains constant, i. e. not exceeding 15 μ.

The next interesting stage in the development of the fleece of thin-wooled sheep is the 65—70 stage. They are then passing through the stage of vigorous formation of hair follicles of the coarse fleece. As early as at 62 days in foetuses appear follicles of the coarse fleece but on the head and partly on the neck. However, already at the age of 70 days the whole body of the foetus is covered wtih coarse-hair rudiments, with a varying degree of the follicle density. Some parts of the body show a more, others a less dense population. Most densely covered (with hair rudiments) is the head, then (according to the rate of density) follow the shoulders, thigh sides, the belly of all parts of the body being most sparsely covered. The rate of follicle population density on body parts depends upon the time, i. e. a thicker covering is seen on those parts of the body, on which follicle formation occurs earlier; this phenomenon was observed by the author in the «kurdyuk» sheep as well.

During the said developmental period, in conjunction with the intensive development of the coat of rudimentary coarse hairs on all parts of the body, a vigorous process of corium thickening is observed at this stage: on the head it attains a thickness of about 250 μ, shoulders 190 μ, back 200 μ, sides 180 μ. It should be pointed out that the vigorous formation of the coarse-hair rudiments in this stage (of embryonic growth) is characteristic of the development of the fleece of fine-wooled sheep alone. In the latter the process of distribution of coarse-hair rudiments over the body is accomplished in 14—15 days. In the «kurdyuk» breed it is considerably slower taking about 30—35 days (²).

Besides, during the 67—70-day period takes place the initial development of the downy hair follicles. They appear first but on the forehead, nearer the poll. They are minute hair rudiments of light colour, clearly distinct from the rudiments of coarse hairs. The first appearance of downy follicles at the same age has been observed in foetuses of the Kirghiz «kurdyuk» sheep (²). The same is described by Galpin in foetuses of the Romney-Marsh breed. The process of the initial formation of fine hair follicles in fine-wooled sheep occurs in the same stage as in the coarse-wooled breed, approximately during the 60—70-day period. At this stage of development occurs the formation of primary groups of hair. At the given age the forehead shows the formation of early hair groups of the trio arrangement. The primary group is one consisting of 3 hair follicles, the arrangement being such that in the center of the group a coarse-hair rudiment is situated with two finer ones placed on the sides. The same initial trio groups have been found by the author at the same

age in foetuses of the Kirghiz «kurdyuk» sheep as well. For this stage Galpin has likewise reported the first trio grouping in Romney-Marsh foetuses. Apparently, the primary trio group is the initial group of hairs both in fine- and coarse-wooled sheep. The age of 72—75 days is characterized in the fine-wooled breed by the vigorous formation during this period of embryogenesis of fine-hair follicles. At this stage all parts of the body become covered with fine-wool rudiments. In coarse-wooled sheep this process takes a slower course. Foetuses of the latter have all body parts covered with fine-hair rudiments not till the end of the third month of embryonic life.

The process of development of fine-hair follicles in fine-wooled sheep takes from 5 to 8 days, whereas in coarse-wooled it is of 20—25 days duration. In 72—75-day foetuses the intensive development of fine hair rudiments is accompanied by a considerable thickness of the corium. The thickness of the latter in a foetus of this age attains 300 μ on the forehead, 200 μ on the shoulder, 200 μ on the back , 250 μ on the thigh. Besides, on the forehead, neck and shoulder of the foetuses appear among rudiments of coarse hairs of early formation new coarse-hair rudiments of late formation, the diameter of the latter being 45 μ. The same phenomenon has been apparent in foetuses of coarse-wooled sheep. They exhibit among the rudiments of coarse hairs of earlier formation rudiments of coarse hairs of later formation. On particular areas of the foetal body the formation of hair follicles of one category of hair proceeds not simultaneously, but successively (2).

In foetuses aged 80—85 days the state of development of the wool covering of the skin differs little from that in 75-day foetuses. An interesting stage in the development of the coat is the 105—107-day one. At this age the foetus is all covered with hairs scarcely piercing the skin not of the same length throughout. The head and the first phalanges are beset with long covering hair. On the neck and thigh the hair is short, though longer than on the back and sides. The belly is covered with sparse long straight hairs. In these foetuses the corium is considerably thickened, its thickness attaining 1000 μ on the forehead, 700 μ on the back and 800 μ on the belly and thigh. When the hairs are piercing the skin, the inner sheath of the coarse hairs is located at a depth of 600 μ, and that of the fine hairs—of 200 μ on the average. It is thereby observed that the longer coarse hairs cover those areas which have a thicker corium.

In 120-day foetuses having the entire body already covered with well formed curls, a still greater thickening of the corium takes place. For instance, on the head it attains a thickness of 2000 μ, on the side 1800 μ, on the back and thigh 1500 μ; there is a parallel downward extension of the root sheath into the depth of the corium. Coarse-hair follicles producing curls are placed in the skin at a depth of 1000 μ, and fine-hair follicles at a depth of 250 μ. The coarse-hair rudiments are implanted at a great depth, extending almost down to the subcutaneous cellular tissue, and the fine-hair follicles are nearer the epidermal layer.

A foetus at the age of 150 days is a completely formed animal with a well grown fine and coarse coat. Coarse hairs are not always present; however, in most foetuses such are observed. The coarse-hair population is not a constant value. Some foetuses have a greater, others a smaller amount of hairs. The coarse hairs are more or less uniformly arranged over the body. For instance, they are more thickly placed on the head, thigh and belly than on other regions of the body. They are less numerous on the sides than on the back. The curl in foetuses is made up of fine hairs, the smaller curls arranging themselves on the sides and caudal part of the back.

Just a few words about the development of the coat. In the pre-natal fleece development of fine-wooled sheep hair-formation does not proceed

at a uniform rate, i. e. the period of more intensive formation of hair follicles is followed by a period of slower formation. For instance, as may be seen from our present and previous work, the rate of development of the follicle population (density) varies in different parts of the foetal body; in some regions the rate is faster, in others slower. Thus, in 75-day foetuses an intensive formation of hair rudiments on the sides takes place, being less intensive on the shoulder, neck and thigh; on the back occurs but an insignificant increase of the follicle population. Within the 105—107-day period of growth the development of the follicle population is uniform throughout the body. In 120-day foetuses a new intensification in the formation of hair rudiments is noted, showing a higher rate on the sides, and a lower one on the shoulder and thigh. A light increase in the follicle population is observed on the back.

In conclusion we should point to some common traits in the development of the coat in fine- and coarse-wooled sheep in the early stages of embryogenesis. It is time and place of originating of follicles of particular hair categories. Rudiments of sensory follicles of coarse and fine hair appear at the same stages of pre-natal development and on the same regions of the body.

The essential feature distinguishing the development of a fine fleece is the considerably faster rate of formation of hair follicles of all categories of hairs on the body of foetuses of fine-wooled sheep.

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